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Ecology of the Podocarpaceae in Tropical Forests

Edited by
Benjamin L. Turner and
Lucas A. Cernusak

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Ecology of the Podocarpaceae in Tropical Forests

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ABSTRACT

Turner, Benjamin L., and Lucas A. Cernusak, editors. *Ecology of the Podocarpaceae in Tropical Forests*. *Smithsonian Contributions to Botany*, number 95, viii + 207 pages, 70 figures, 18 tables, 2011.—The emergence of angiosperms in tropical forests at the expense of the gymnosperms, their ancestral relatives, was one of the most important events in the evolutionary history of terrestrial plants. Gymnosperms were nearly eliminated from the tropics after the evolution of angiosperms in the early Cretaceous, yet conifers of the Podocarpaceae are among the few gymnosperm families that persist in tropical forests worldwide. Podocarps are often considered to be restricted to montane sites in the tropics, a feature of their biogeography that is used by paleoecologists to reconstruct past forest communities. However, podocarps also occur in the lowland tropics, where they can be the dominant component of forest canopies. Podocarps have proved to be remarkably adaptable in many cases: members of the family have a semi-aquatic lifestyle, exhibit drought tolerance and resprouting, and include the only known parasitic gymnosperm. Other intriguing aspects of podocarp physiology include the mechanism of water transport in the leaves and the conspicuous root nodules, which are not involved in nitrogen fixation but instead house arbuscular mycorrhizal fungi. Perhaps most surprising, paleobotanical evidence indicates that far from being ‘relict’ members of tropical forest communities, podocarps have been dispersing into the tropics since the late Eocene epoch more than 30 million years ago. These and other aspects of the Podocarpaceae explored in this volume have far-reaching implications for understanding the ecology and evolution of tropical rain forests.

Cover images: Left, nodules and root hairs on *Prumnopitys ferruginea* (see chapter 11); center, seedlings of *Podocarpus guatemalensis* growing in a shadehouse in Panama (see chapter 3); right, the semi-aquatic podocarp *Retrophyllum minus* growing in a stream in New Caledonia (see chapter 4). Photo credits, left to right: I. A. Dickie, A. W. Cheesman, and J. W. Dalling.

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Contents

PREFACE	v
ACKNOWLEDGMENTS	vii
SECTION I – EVOLUTIONARY HISTORY	
1 Podocarp Evolution: A Molecular Phylogenetic Perspective <i>Edward Biffin, John G. Conran, and Andrew J. Lowe</i>	1
2 Dispersal and Paleoecology of Tropical Podocarps <i>Robert J. Morley</i>	21
SECTION II – DISTRIBUTION AND ECOLOGY OF TROPICAL PODOCARPS	
3 Ecology and Distribution of Neotropical Podocarpaceae <i>James W. Dalling, Phoebe Barkan, Peter J. Bellingham, John R. Healey, and Edmund V. J. Tanner</i>	43
4 Ecology and Distribution of the Malesian Podocarps <i>Neal J. Enright and Tanguy Jaffré</i>	57
5 Podocarps in Africa: Temperate Zone Relicts or Rainforest Survivors? <i>Hylton Adie and Michael J. Lawes</i>	79
6 The Ecology of Podocarps in Tropical Montane Forests of Borneo: Distribution, Population Dynamics, and Soil Nutrient Acquisition <i>Kanehiro Kitayama, Shin-ichi Aiba, Masayuki Ushio, Tatsuyuki Seino, and Yasuto Fujiki</i>	101

SECTION III – A TEMPERATE PERSPECTIVE

- | | | |
|---|--|-----|
| 7 | Temperate and Tropical Podocarps: How Ecologically Alike Are They?
<i>David A. Coomes and Peter J. Bellingham</i> | 119 |
| 8 | Ecology of Fire-Tolerant Podocarps in Temperate Australian Forests
<i>Philip G. Ladd and Neal J. Enright</i> | 141 |

SECTION IV – ECOPHYSIOLOGY AND ENVIRONMENT

- | | | |
|----|---|-----|
| 9 | Conifer–Angiosperm Interactions: Physiological Ecology and Life History
<i>Christopher H. Lusk</i> | 157 |
| 10 | A Functional Analysis of Podocarp Ecology
<i>Timothy J. Brodribb</i> | 165 |
| 11 | Podocarp Roots, Mycorrhizas, and Nodules
<i>Ian A. Dickie and Robert J. Holdaway</i> | 175 |

SECTION V – SYNTHESIS

- | | | |
|----|---|-----|
| 12 | Podocarpaceae in Tropical Forests: A Synthesis
<i>Lucas A. Cernusak, Hylton Adie, Peter J. Bellingham, Edward Biffin, Timothy J. Brodribb, David A. Coomes, James W. Dalling, Ian A. Dickie, Neal J. Enright, Kanehiro Kitayama, Philip G. Ladd, Hans Lambers, Michael J. Lawes, Christopher H. Lusk, Robert J. Morley, and Benjamin L. Turner</i> | 189 |
|----|---|-----|

SUBJECT INDEX	197
---------------	-----

INDEX OF SCIENTIFIC NAMES	203
---------------------------	-----

Preface

The emergence of angiosperms in tropical forests at the expense of the gymnosperms, their ancestral relatives, was one of the most important events in the evolutionary history of terrestrial plants. Although gymnosperms were an important component of the flora on the supercontinent of Gondwana, they were virtually eliminated from the tropics following the evolution of angiosperms in the Early Cretaceous. Modern tropical forests are overwhelmingly dominated by angiosperms, yet a few gymnosperms persist. What can they tell us about the ecology of tropical forests?

Conifers of the Podocarpaceae are one of the few gymnosperms that inhabit tropical forests worldwide, although they remain the least well known of the three large conifer families. Podocarps occur throughout the Malesian, African, and neotropics and are common in temperate regions of Africa, Australasia, and South America. Tropical podocarps are often considered to be restricted to montane sites, a feature of their biogeography that is used by paleoecologists to reconstruct past forest communities. Yet they also occur in the lowland tropics, usually as rare individuals, but sometimes forming the dominant component of forest canopies.

In many cases podocarps have proved to be remarkably adaptable: members of the family have a semiaquatic lifestyle (*Retrophyllum minus*), exhibit drought tolerance and resprouting (*Podocarpus drouynianus*), and include the only known parasitic gymnosperm (*Parasitaxus usta*). Other intriguing aspects of their physiology include the mechanism of water transport in the leaves and the conspicuous root nodules, which are not involved in nitrogen fixation, but instead house arbuscular mycorrhizal fungi. Perhaps most surprising, paleobotanical evidence indicates that far from being “relict” members of tropical forest communities, podocarps have been dispersing actively into the tropics since the late Eocene epoch more than 30 million years ago. Clearly, there is much to be learned from tropical podocarps.

Arising from a workshop held at Macquarie University, Sydney, in February 2009, this volume explores in detail the ecology of the Podocarpaceae in tropical forests. Three main themes are covered:

1. phylogeny and paleohistory of the Podocarpaceae in the tropics (chapters 1 and 2);
2. current distribution of podocarps in the African, American, and Asian tropics (chapters 3–6); and
3. ecology and ecophysiology of the Podocarpaceae in both temperate and tropical ecosystems (chapters 7–11).

The volume concludes with a short synthesis that concisely summarizes the key conclusions of the workshop. The outcome is a truly interdisciplinary review of tropical podocarps, which we hope will inspire further research on these fascinating trees.

A NOTE ON NOMENCLATURE

The taxonomy of the podocarps is complex and the least understood of the three major conifer families, with many synonyms, recent revisions, and additions that are likely to continue in the near future. Here we have followed the nomenclature of Farjon (2001) with the exception of *Parasitaxus usta* in place of *Parasitaxus ustus* (T. Jaffré,

UMR AMAP Institut de Recherche pour le Développement (IRD), Laboratoire de Botanique et d'Ecologie Végétale, Nouméa, New Caledonia, personal communication, November 2009). We also include *Phyllocladus* here as a podocarp; the status of this genus has been controversial, but its elevation to family level as Phyllocladaceae is not supported by phylogenetic analyses, as outlined in chapter 1 of this volume. Finally, we use the term “tropical” here in a strict geographical sense, defined as the area between the Tropics of Cancer and Capricorn. The term should not be taken as synonymous with tropical climate, the extent of which has varied markedly in relatively recent geological history.

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Podocarp Evolution: A Molecular Phylogenetic Perspective

*Edward Biffin, John G. Conran,
and Andrew J. Lowe*

ABSTRACT. Phylogenetic reconstructions of the relationships among extant taxa can be used to infer the nature of the processes that have generated contemporary patterns of biotic diversity. In this study, we present a molecular phylogenetic hypothesis for the conifer family Podocarpaceae based upon three DNA fragments that have been sampled for approximately 90 taxa. We use Bayesian relaxed-clock methods and four fossil constraints to estimate divergence times among the lineages of Podocarpaceae. Our dating analyses suggest that although the family is old (Triassic–Jurassic), the extant species groups are of recent evolutionary origin (mid- to late Cenozoic), a pattern that could reflect a temporal increase in the rate lineage accumulation or, alternatively, a high and constant rate of extinction. Our data do not support the hypothesis that Podocarpaceae have diversified at a homogeneous rate, instead providing strong evidence for a three- to eightfold increase in diversification associated with the Podocarpoid–Dacrydioid clade, which radiated in the mid- to late Cretaceous to the earliest Cenozoic, around 60–94 MYA. This group includes a predominance of taxa that develop broad leaves and/or leaf-like shoots and are distributed predominantly throughout the tropics. Tropical podocarps with broad leaves may have experienced reduced extinction and/or increased speciation coincident with the radiation of the angiosperms, the expansion of megathermal forests, and relatively stable tropical climates that were widespread through the Tertiary.

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INTRODUCTION

Patterns of species diversity reflect the balance of speciation and extinction over the evolutionary history of life. These, in turn, are parameters influenced by extrinsic factors, such as environmental condition and long-term processes of geological and climatic change, and intrinsic attributes of organisms, such as morphological innovations that increase the propensity for speciation or reduce the risk of extinction. The key aims of evolutionary biologists are to

explain patterns of diversity and, foremost, to determine whether there is evidence for significant heterogeneity in the “per lineage” patterns of diversity that require explanation (Sanderson and Wojciechowski, 1996; Magallón and Sanderson, 2001; Davies et al., 2004; Moore and Donoghue, 2007; Rabosky et al., 2007). Phylogenetic reconstructions of evolutionary relationships provide an indirect record of the speciation events that have led to extant species. Because evolutionary rates can be estimated from phylogenetic data, such reconstructions can help to elucidate the significance and drivers of biotic diversity patterns (Moore and Donoghue, 2007; Ricklefs, 2007).

Molecular phylogenetics has revolutionized the field of evolutionary biology. For instance, the molecular clock hypothesis predicts that the level of genetic divergence between any two lineages will be proportional to the time since divergence from a most recent common ancestor. Therefore, using external calibrations (e.g., timing of vicariance events, fossils of known age, and phylogenetic affinity) or known mutation rates, it is possible to estimate the age of all of the splits in a molecular phylogenetic tree (which often comprise a majority of splits with no associated fossil data to directly estimate the age). There has been justified criticism of the molecular clock hypothesis. In particular, there is strong evidence that in most lineages, the constancy of mutation rates in proteins or DNA sequences cannot be assumed (e.g., Ayala, 1997; Bromham and Penny, 2003). Recently developed methods, which attempt to incorporate heterogeneity into phylogenetic analysis by specifying a model of rate variation among lineages (referred to as relaxed-clock methods), are believed to provide more realistic estimates of divergence times in the absence of rate constancy (for recent reviews see Bromham and Penny, 2003; Rutschmann, 2006). Furthermore, there have been promising developments in methods to account for uncertainty inherent in the fossil record; Bayesian methods, in particular, can incorporate fossil calibrations because parametric prior probability distributions make fewer assumptions (relative to “fixed”-point calibrations) concerning the nodal placement of a given fossil datum on a phylogenetic tree (Yang and Rannala, 2006; Sanders and Lee, 2007). With improved confidence in hypotheses, there has been a diversification of questions and associated methodologies developed around molecular clock phylogenies. These include the examination of vicariance versus dispersal explanations for diversity patterns (e.g., Crisp and Cook, 2007), the timing of evolutionary radiations and/or extinctions and coincidence with environmental change (e.g., Davis et al., 2005), and estimation of the tempo of diversification using a statistical framework to contrast

phylogenetic data with null expectations (e.g., Rabosky et al., 2007; Rabosky and Lovette, 2008).

The conifer family Podocarpaceae comprises approximately 173 species and 18 genera (Farjon, 1998) distributed primarily in the Southern Hemisphere, although extending northward as far as subtropical China and Japan and to Mexico and the Caribbean (see Enright and Jaffré, this volume; Dalling et al., this volume). The podocarps have a rich fossil record that suggests an origin in the Triassic and a distribution in both the Northern and Southern hemispheres through the Mesozoic, although by the Cenozoic the fossil record of the family is overwhelmingly southern (Hill and Brodribb, 1999). Currently, the Podocarpaceae comprise a majority of species-poor (Figure 1.1), range-restricted genera (e.g., *Acmopyle*, *Lagarostrobos*, *Microcachrys*, *Microstrobos*, *Saxegothea*) that are presumably relictual, as evidenced by the fossil record, which indicates broader distributions and greater species diversities in the past (Hill and Brodribb, 1999). Relatively few genera are species rich and widely distributed, although *Podocarpus* comprises approximately 105 species (Figure 1.1) and occurs on all continents except Antarctica and Europe.

“Nearest living relative” comparisons of Podocarpaceae suggest the conservation of morphology, community associations, and ecological response over evolutionary time (Brodribb and Hill, 2004). From this perspective, the Podocarpaceae provide an outstanding opportunity to explore the influences of organism–environment interactions in the context of large-scale geological and climatic change in shaping patterns of extant distribution and diversity. For example, the majority of podocarp species presently occur within angiosperm-dominated humid forests. This pattern is of considerable interest to paleobotanists, ecologists, and biogeographers (e.g., Brodribb and Hill, 2004; Brodribb and Feild, 2008), given that conifers in general have been considered less competitive than angiosperms in productive environments (Bond, 1989). Using the ecophysiological tolerances of extant species as representative of closely allied extinct fossil taxa, it has been argued that characteristics such as leaf flattening and associated physiologies have promoted the persistence of Podocarpaceae in the face of angiosperm competition (Brodribb and Hill, 1997; Brodribb and Feild, 2008). However, within Australia, these characteristics may also be associated with range contraction and at least local extinction of several lineages as a consequence of increasing aridity in the Miocene–Pliocene (Hill and Brodribb, 1999; Brodribb and Hill, 2004).

Here we use molecular (DNA sequence) data, first, to assess phylogenetic relationships among Podocarpaceae and, second, using a relaxed molecular clock approach, to estimate the timing of diversification events for the major

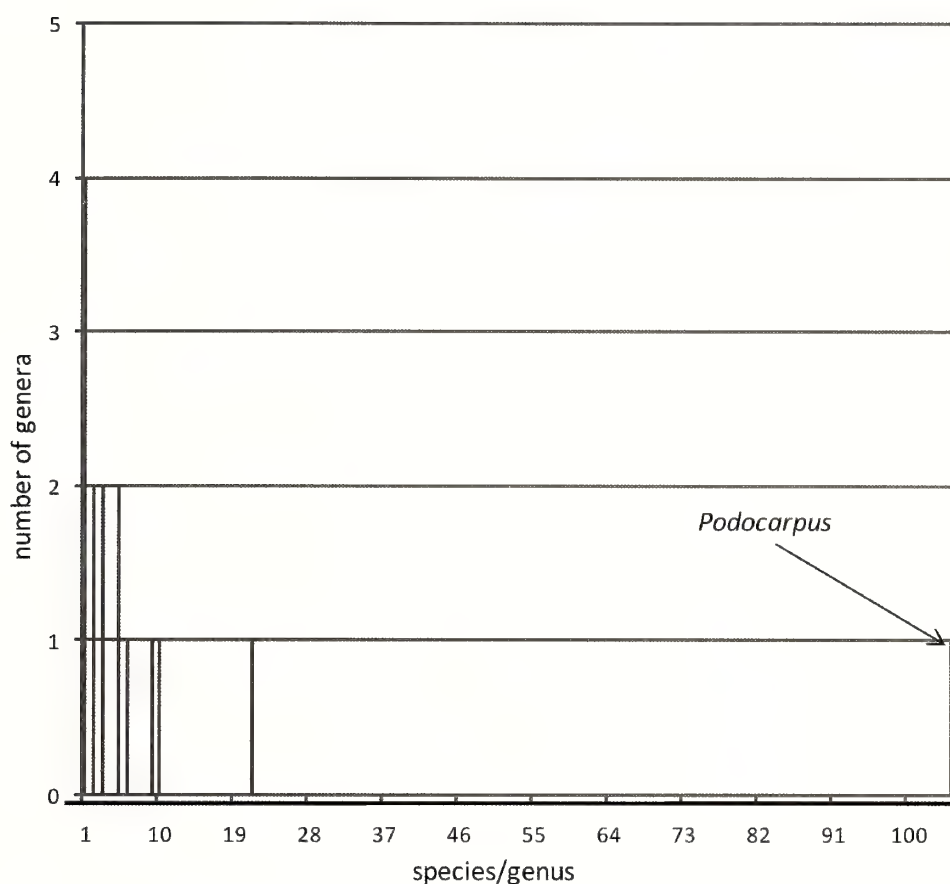


FIGURE 1.1. Frequency distribution of species/genus for the Podocarpaceae (estimates according to Farjon, 1998).

lineages. From this perspective we explore macroevolutionary patterns within the family and specifically use the dated molecular phylogeny to test whether it is necessary to invoke among-lineage variation in diversification rates to explain the disparities in extant diversity among major groups of Podocarpaceae. Our results indicate a highly significant shift in diversification rates corresponding to approximately the Cretaceous–Tertiary boundary. The significance of this diversification rate shift is briefly explored in the context of the angiosperm radiation, biogeography, and ecophysiology.

PHYLOGENETIC RELATIONSHIPS IN THE PODOCARPACEAE

PREVIOUS STUDIES

There have been several previous phylogenetic studies of the Podocarpaceae, including those based upon

morphology (Hart, 1987; Kelch, 1997, 1998) and molecular (DNA sequence) data (Kelch, 1998, 2002; Conran et al., 2000; Sinclair et al., 2002). A key focus of these studies has been the assessment of relationships for classification; for instance, the status of *Phyllocladus* has been controversial, although the elevation of this taxon to family level as Phyllocladaceae (e.g., Page, 1990a; Bobrov et al., 1999) is not supported by phylogenetic analyses to date (Conran et al., 2000; Quinn et al., 2002; Sinclair et al., 2002; Wagstaff, 2004; Rai et al., 2008). More generally, there have been conflicting results from morphological versus molecular data; for example, the morphological analyses reported in Kelch (1997) suggest that gross leaf morphology is a reasonable predictor of evolutionary relationships in the Podocarpaceae, whereas analyses of DNA sequences found that scalelike leaves were polyphyletic on the estimated topologies (Kelch, 1998; Conran et al., 2000; Sinclair et al., 2002). In this instance, there are, perhaps, reasonable grounds to favor the molecular over the morphological data, given the generally poor support

for relationships from morphology, and in contrast to the molecules, the morphological data are not entirely independent of the conclusions (i.e., leaf morphologies were included as characters). From a wide range of studies, issues with morphology include fewer variable characters compared to DNA sequences and homoplasy, which may be a consequence of the choice of characters and character construction (i.e., homology assessment) as much as convergent or parallel evolution (Givnish and Sytsma, 1997; Scotland et al., 2003). Nevertheless, morphological data will continue to be important in reconstructing phylogeny; for instance, they provide the only readily sourced information on extinct fossil taxa (Wiens, 2004).

Phylogenetic studies to date have focused predominantly on generic relationships among members of the Podocarpaceae, but Hart (1987) and Kelch (1997) included, at best, a single taxon per genus, with a view to resolving deeper branches of the podocarp phylogeny. The studies of Conran et al. (2000), Kelch (2002), and Sinclair et al. (2002) included denser taxon sampling, so that generic monophyly could be assessed. Encouragingly, the evidence from both chloroplast and nuclear DNA is consistent with contemporary generic schemes (e.g., Page, 1988, 1990b; Farjon, 1998), although there are a few minor exceptions. For example, *Sundacarpus* is nested within *Prumnopitys* with strong statistical support, according to Sinclair et al. (2002).

DATA AND PHYLOGENETIC METHODS

There is a range of evolutionary questions that are best addressed using complete, or near complete, sampling of species, which is the eventual aim of the authors. In the present context, we present a preliminary phylogenetic analysis of the Podocarpaceae using a data set comprising 89 taxa (including two Araucariaceae as an out-group) that have been sequenced for two chloroplast genes (*matK* gene and the *trnL-trnF* intron and spacer region) and internal transcribed spacer 2 of nuclear ribosomal DNA (ITS2). Data not sourced from GenBank were sequenced de novo (Table 1.1). For sequencing methods, the reader is referred to Quinn et al. (2002; *matK*) and Sinclair et al. (2002; *trnL-trnF* and ITS2) and to Table 1.2, which details the primer combinations used for each fragment. Sequence alignment was performed using ClustalW (Thompson et al., 1994) and manual (“by eye”) adjustment. The aligned data matrix is available from the authors upon request. The molecular data were analyzed using Bayesian phylogenetic methods (as implemented in MrBayes version 3.1.2; Ronquist and Huelsenbeck, 2003). In the first instance, each of

the *matK*, *trnL-trnF* intron and spacer, and ITS2 sequence alignments was analyzed separately, assuming a general time reversible (GTR) model of sequence evolution with Γ distributed rate variation among sites, and a proportion of sites were considered invariant (I) (run conditions as below). The topologies from each of the separate analyses were visually inspected to identify well-supported (posterior probability (PP) ≥ 0.95 ; i.e., the grouping is found in $\geq 95\%$ of the topologies sampled from the PP distribution) but conflicting resolutions among individual data sets (none found), and the data were concatenated and analyzed in combination using partitioned Bayesian analyses (i.e., topologies were derived by allowing each of the separate data partitions to evolve its best-fit set of GTR model parameters). Topologies were estimated from four independent runs of 1×10^6 generations, sampling topology, and parameter values every hundredth generation, each with four starting chains (one cold, three heated). Convergence was assessed relative to the variance in parameter estimates between independent runs and by inspection of the convergence diagnostics that are summarized using the “sump” command in MrBayes. Majority rule consensus trees were generated using the “sumt” command, discarding trees generated during the burn-in, with the burn-in proportion determined by inspection of the convergence diagnostics.

Some studies have reported high Bayesian posterior probability values corresponding to relatively weaker clade support from nonparametric bootstrapping (BS) for the same data set (see Alfaro et al., 2003, and references therein). In addition to Bayesian analyses, we used the maximum likelihood (ML) implementation GARLI (Zwickl, 2006) to estimate support for podocarp relationships. For these analyses, we used the concatenated alignment, a GTR + I + Γ model of sequence evolution with parameter values estimated from the data, and we performed 100 BS pseudoreplicates to estimate clade support.

PHYLOGENETIC RELATIONSHIPS OF THE PODOCARPACEAE

The Bayesian majority rule consensus topology from the concatenated data analyses is presented in Figure 1.2. We recovered generally consistent topologies from Bayesian and ML analyses in terms of both resolution and statistical support: clades receiving a PP > 0.95 also had ML BS values of $> 80\%$, and there were no strongly supported conflicting resolutions among criteria. As with previous molecular phylogenies of the Podocarpaceae, the conventionally recognized genera are strongly supported as monophyletic, with the exception of *Prumnopitys*, which includes

TABLE 1.1. Taxon sampling for DNA sequences. GenBank accession numbers are listed. An asterisk (*) indicates de novo sequencing; a dash (-) indicates missing data; and ITS2 = internal transcribed spacer 2.

Taxon	<i>matK</i>	<i>trnL-trnF</i>	ITS2
Podocarpaceae			
<i>Acropyle pancheri</i> (Brong. & Gris) Pilger	*	AY083141/AY083097	AY083057
<i>A. sabniana</i> Buchholz & N. E. Gray	*	*	*
<i>Afrocarpus falcatus</i> (Thunb.) C. N. Page	AF457111	*	*
<i>A. gausseii</i> (Woltz) C. N. Page	-	AY083145/AY083101	AY083061
<i>A. gracilior</i> (Pilg.) C. N. Page	-	*	*
<i>A. mannii</i> (Hooker f.) C. N. Page	*	*	*
<i>Dacrycarpus cinctus</i> (Pilger) de Laub.	*	*	*
<i>D. compactus</i> (Wasscher) de Laub.	*	*	AY083055
<i>D. dacrydioides</i> (A. Rich) de Laub.	*	*	*
<i>D. imbricatus</i> (Blume) de Laub.	*	*	*
<i>D. veillardii</i> (Parl.) de Laub.	*	*	*
<i>Dacrydium araucarioides</i> Brogn. & Gris	-	AY083138/AY083094	AY083054
<i>D. balanse</i> Brogn & Gris	*	*	*
<i>D. cupressinum</i> Soland. ex Lamb.	AF457112	AY03136/AY083092	AY083052
<i>D. guillauminii</i> Buchholz	*	*	*
<i>D. lycopodioides</i> Brongniart et Grisebach	*	*	*
<i>D. nausoriense</i> de Laub.	*	*	*
<i>D. nidulum</i> de Laub.	*	*	*
<i>Falcatifolium falciforme</i> (Parl.) de Laub.	*	*	*
<i>F. gruezoii</i> de Laub.	-	AY083144/AY083100	AY083060
<i>F. taxoides</i> (Brongn. & Gris) de Laub.	-	AY083143/AY083099	AY083059
<i>Halocarpus bidwillii</i> (Hook. f. ex Kirk) Quinn	*	AY083128/AY083084	AY083044
<i>H. biformis</i> (Hook.) Quinn	*	AY083129/AY083085	AY083045
<i>H. kirkii</i> (F. Muell ex Parl.) Quinn	AF457117	AY083130/AY083086	AY083046
<i>Lagarostrobos franklinii</i> (Hook. f.) Quinn	*	AY083132/AY083088	AY083048
<i>Lepidothamnus fonkii</i> Phil. S. Wagstaff	-	AY083119/AY083075	AY083035
<i>L. laxifolius</i> (Hook. f.) Quinn	AF457114	AY083120/AY083076	AY083036
<i>Manoao colensoi</i> (Hook.) Molloy	*	*	*
<i>Microcachrys tetragona</i> (Hook.) Hook. f.	*	AY083134/AY083090	AY083050
<i>Microstrobos fitzgeraldii</i> (F. Muell.) J. Garden & L. A. S. Johnson	*	AY083135/AY083091	AY0835051
<i>M. niphophilus</i> J. Garden & L. A. S. Johnson	*	*	*
<i>Nageia fleuryi</i> (Hickel) de Laub.	*	*	*
<i>N. formosensis</i> (Dummer) C. N. Page	*	*	*
<i>N. nagi</i> (Thunb.) O. Kuntze H. Katsurada	AF228112	AY083147/AY083103	AY083063
<i>N. wallichiana</i> (Presl.) O. Kuntze	*	*	*
<i>Parasitaxus ustus</i> (Veillard) de Laub.	*	AY083131/AY083087	AY083047
<i>Phyllocladus alpinus</i> Hook. f. Wardle	AY442146	-	AY442160
<i>P. aspleniifolius</i> (Labill.) Hook. f.	AY442147	AY083117/AY083073	AY442167
<i>P. hypophyllum</i> Hook. f. J. Read	AY442148	AY083116/AY083072	AY442156
<i>P. toatoa</i> Molloy	AY442149	-	AY442163
<i>P. trichomanoides</i> D. Don ex Cunn.	AY442150	AY083118/AY083074	AY442165
<i>Podocarpus affinis</i> Seem.	*	*	*
<i>P. alpinus</i> R. Br. ex Hook. f.	*	*	*
<i>P. annamiensis</i> N. E. Gray	-	*	*
<i>P. aristulatus</i> Parl.	*	*	*

continued

TABLE 1.1. (Continued)

Taxon	<i>matK</i>	<i>trnL-trnF</i>	ITS2
Podocarpaceae			
<i>P. brassii</i> Pilger in Engler	*	*	-
<i>P. chinensis</i> (Roxb.) Wall. ex Forbes	*	*	*
<i>P. costalis</i> C. Presl.	*	*	*
<i>P. cunninghamii</i> Colenso	-	*	*
<i>P. dispermus</i> White	*	*	*
<i>P. drouynianus</i> F. Muell.	*	*	*
<i>P. elatus</i> R. Br. ex Endl.	AF457113	*	*
<i>P. elongatus</i> (Aiton) L'Herit. ex Persoon	*	*	-
<i>P. gnidioides</i> Carrière	*	*	*
<i>P. guatemalensis</i> Standl.	-	AY083151/AY083107	AY083067
<i>P. henkelii</i> Stapf	*	*	AY845209
<i>P. lambertii</i> Klotzsch ex Endl.	*	*	*
<i>P. latifolius</i> (Thunb.) R. Br. ex Mirb.	-	*	AY845215
<i>P. lawrencei</i> Hook. f.	*	*	*
<i>P. lawrencei</i>	*	*	*
<i>P. lawrencei</i>	*	*	*
<i>P. lawrencei</i>	*	*	*
<i>P. longifoliolatus</i> Pilger in Engler	*	AY083149/AY083105	AY083065
<i>P. macrophyllus</i> (Thunb.) Sweet	AF228111	*	*
<i>P. matudae</i> Lundell	*	*	*
<i>P. neriifolius</i> D. Don in Lamb.	*	*	*
<i>P. nivalis</i> Hook. f.	*	*	*
<i>P. nubigenus</i> Lindley	*	*	*
<i>P. polystachyus</i> R. Br. ex Endl.	*	*	*
<i>P. rumphii</i> Blume	*	*	*
<i>P. salignus</i> D. Don	*	AY083148/AY083104	AY083064
<i>P. smithii</i> de Laub.	-	*	*
<i>P. spinulosus</i> (Smith) R. Br.	*	*	*
<i>P. sylvestris</i> J. Buchholz	*	AY083152/AY083108	AY083068
<i>P. totara</i> D. Don	*	*	*
<i>Prumnopitys andina</i> (Poepp. ex Endl.) de Laub.	*	AY083124/AY083080	AY083040
<i>P. ferruginea</i> (D. Don) de Laub.	AF457115	AY083127/AY083083	AY083043
<i>P. ferruginoides</i> (Compton) de Laub.	*	AY083126/AY083082	AY083042
<i>P. ladei</i> (Bailey) de Laub.	*	AY083125/AY083081	AY083041
<i>P. taxifolia</i> (Soland. ex D. Don) de Laub.	*	AY083123/AY083079	AY083039
<i>Retrophyllum comptonii</i> (Buchh.) C. N. Page	-	*	*
<i>R. vitiense</i> (Seeman) C. N. Page	*	*	*
<i>Saxegothaea conspicua</i> Lindl.	AF457116	AY083121/AY083077	AY083037
<i>Sundacarpus amarus</i> (Blume) C. N. Page	*	AY083122/AY083078	AY083038
Araucariaceae			
<i>Agathis australis</i> (D. Don) Loudon	EU025980	AY083115/AY083071	AY083031
<i>Araucaria heterophylla</i> (Salisb.) Franco	AF456374	-	*
<i>Araucaria biramulata</i> Buchholz	-	AY083114/AY083070	-

TABLE 1.2. PCR and sequencing primers.

Region	Name	Sequence 5'-3'	Reference
<i>matK</i>	matkF1	AAYAARCATAGATCTTGGCARCAAT	This study
<i>matK</i>	matkF2	TGYGAATCCATTHTAGTTCCYCTT	This study
<i>matK</i>	matKR1	AGSRATCTTTCBCSRTATCTCACATA	This study
<i>matK</i>	matKR2	TTAGCRCATGAAAGTAGAAGTA	This study
<i>trnL-trnF</i>	TabC	CGAAATCGGTAGACGCTACG	Taberlet et al. (1991)
<i>trnL-trnF</i>	TabF	TITGAACTGGTGACACGAG	Taberlet et al. (1991)
ITS2	ITS3P	GCCACGATGAAGAACGTAGCGA	Modified from White et al. (1990)
ITS2	ITS4P	CCGCTTATTGATATGCTTAAGCTCA	Modified from White et al. (1990)

Sundacarpus (*Prumnopitys* sensu lato). The relationships among genera are also largely well supported. Strongly supported groupings include a “Podocarpoid” clade (*Afrocarpus*, *Nageia*, *Podocarpus*, *Retrophyllum*), a “Dacrydioid” clade (*Dacrydium*, *Dacrycarpus*, *Falcatifolium*), and a “Prumnopityoid” clade (*Halocarpus*, *Lagarostrobos*, *Manoao*, *Parasitaxus*, *Prumnopitys* sensu lato) (Figure 1.2). These groupings were previously recovered by Conran et al. (2000), although with relatively weak support. At a lower taxonomic level, resolutions include the pairing of *Manoao* and *Lagarostrobos*, with *Parasitaxus* sister to these, a relationship that was suggested, but not statistically supported, in the analyses of Sinclair et al. (2002). Given the level of divergence, the segregation of *Manoao* from *Lagarostrobos* is reasonable on the basis of the present data, as is that of *Falcatifolium* from *Dacrydium* sensu stricto (cf. Conran et al., 2000). The deepest branches in the phylogeny are not strongly supported, although a group including *Lepidothamnus*, *Phyllocladus*, and the Prumnopityoid clade has a PP of 0.91 and a BS and ML bootstrap support of 60%, and the pairing of *Lepidothamnus* and *Phyllocladus* is also weakly supported (PP = 0.79, BS = 68%).

Although genera, and most intergeneric relationships, receive strong support from these data, relationships among species are relatively ambiguous. For instance, all resolutions within *Afrocarpus*, *Dacrycarpus*, *Nageia*, and *Phyllocladus* are, at best, weakly supported (PP ≤ 0.9), whereas within *Dacrydium* and *Podocarpus* the majority of nodes receive low levels of statistical support. On one hand, poor resolution may be a consequence of data conflict (i.e., individual data sets support conflicting resolutions), leading to topological ambiguity. Alternatively, there may be insufficient evidence to adequately resolve relationships, analogous to sampling error in small data sets (Graham et al., 1998). As noted above, there were

no strongly supported conflicting resolutions noted in the visual inspection of topologies derived from individual data partitions, suggesting that the latter is a reasonable hypothesis. Furthermore, as the data are not uninformative per se, it could be argued that poor resolution among species is a consequence of relatively recent radiations, such that lineages have had insufficient time to accrue informative mutations. Typically, this scenario is associated with a broomlike topology (as discussed by Crisp et al., 2004), which is evident in the present data. Low-level studies of *Afrocarpus* (Barker et al., 2004), *Phyllocladus* (Wagstaff, 2004), and *Retrophyllum* (Herbert et al., 2002) report similarly poor resolution among species, consistent with relatively recent origins (see Wagstaff, 2004, who explicitly considers divergence time estimates). The timing of radiations within the Podocarpaceae is addressed further in the next section.

MOLECULAR DATING ANALYSES

In the present study, we use the Bayesian relaxed-clock implementation in BEAST (Drummond and Rambaut, 2007) to estimate divergence times among lineages of the Podocarpaceae. BEAST uses a probabilistic model to describe the pattern of change in molecular rates through time and Markov chain Monte Carlo (MCMC) simulation sampling substitution rates, branch lengths, the individual parameters of the substitution model, and tree priors to derive the posterior probability of divergence time estimates (Drummond et al., 2006; Rutschmann, 2006). In contrast to other currently available molecular dating implementations, BEAST samples both tree topology and branch lengths, allowing the user to coestimate phylogeny and substitution rates. Departures from the molecular clock

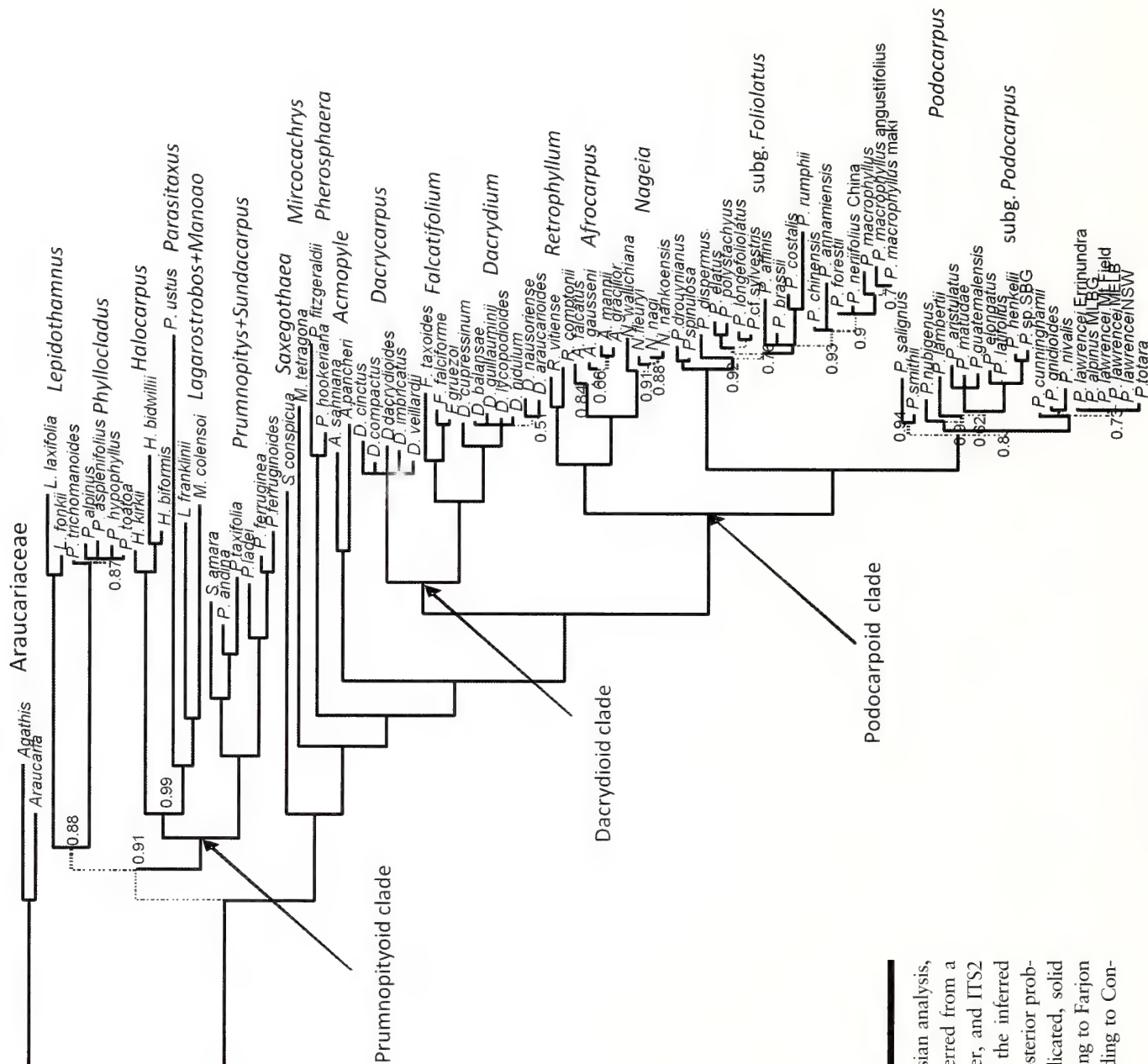


FIGURE 1.2. Phylogenetic relationships (Bayesian analysis, 50% majority rule) in the Podocarpaceae inferred from a *matK*, *trnL-trnF* chloroplast intron and spacer, and ITS2 data set. Branch lengths are proportional to the inferred number of changes; dashed branches have a posterior probability (PP) < 0.95, and unless otherwise indicated, solid branches have a PP of 1.0. Genera are according to Farjon (1998), and higher-order groupings are according to Conran et al. (2000).

assumption are estimated from the data, with completely clocklike (i.e., a single rate across the tree) to highly heterogeneous (i.e., numerous rate changes among branches) models representing the opposite extremes of a spectrum of rate variation (Drummond et al., 2006).

In BEAST, fossil calibrations are incorporated as prior probability distributions, including parametric distributions such as normal, lognormal, or exponential prior probabilities on the distribution of node ages. Given that many (if not most) fossil placements have a degree of uncertainty, this approach has advantages over the incorporation of fossil data as “fixed”-point calibrations on a particular node (see, e.g., Yang and Rannala, 2006; Benton and Donoghue, 2007; Sanders and Lee, 2007). For instance, a prior probability distribution can be designed with a peak probability corresponding to the age of a fossil and with decreasing, but nonzero, probabilities that the calibration node is either older or younger than the fossil age distributed according to a normal distribution (Sanders and Lee, 2007).

Divergence time estimates were derived from a chloroplast data set comprising the *matK* coding region and *trnL-trnF* spacer and intron for 92 taxa (90 representatives of the Podocarpaceae and 2 representatives of the Araucariaceae). Four fossil-derived constraints were used to calibrate molecular rates (Table 1.3). These were selected

from the literature (e.g., Hill and Brodribb, 1999) on the basis of the oldest reasonably placed macrofossil age for the associated lineage. The incompleteness of the fossil record usually requires that a fossil assigned to a particular node provides the minimum age for that node (i.e., older fossils may yet be found), although fossil age constraints are often applied to the node that subtends the crown group, which may be significantly younger than the actual age of the fossil lineage (Magallón and Sanderson, 2001; Magallón, 2004; Renner, 2005). Where the accuracy of fossil placement is uncertain the most objective calibration method may be to fix the stem group (age) as the minimum age for the diversification of the descendant crown group (given that the fossil in question is correctly assigned to a lineage; Renner, 2005). In other words, the stem group node must be at least as old or older than a fossil belonging to that lineage. Maximum (upper) constraints are more difficult to establish (Benton and Donoghue, 2007), although a “soft” upper bound (i.e., with nonzero probabilities associated with all reasonable values) can be defined using an appropriate parametric distribution (Yang and Rannala, 2006; Sanders and Lee, 2007).

In the present study, the fossil-derived dates were used to provide the minimum age for the most recent common ancestor of the corresponding stem group. Uncertainty in the association between the calibration node and the fossil

TABLE 1.3. Fossil calibration points used for divergence time estimation. Calibration node numbers correspond to Figure 1.3. Abbreviations: CI, confidence interval; HPD, highest posterior density.

Calibration node	Reference	Fossil age	Translated lognormal prior (median, 95% CI)	Posterior (median, 95% HPD of node age)
1. Dacrydioid clade (<i>Dacrycarpus</i> , <i>Dacrydium</i> , <i>Falcatifolium</i>)	<i>Dacrycarpus linifolius</i> Wells and Hill emend. Hill and Carpenter (Hill and Carpenter, 1991) <i>D. mucronatus</i> Wells and Hill emend. Hill and Carpenter (Wells and Hill, 1989; Hill and Carpenter, 1991)	Early Eocene	60 (50–102)	62 (51–76)
2. Podocarpid clade (<i>Afrocarpus</i> , <i>Nageia</i> , <i>Podocarpus</i> , <i>Retrophyllum</i>)	<i>Podocarpus strzeleckianus</i> Townrow (Townrow, 1965)	Early Eocene	60 (50–102)	57 (49–67)
3. Prumnopityoid clade (<i>Halocarpus</i> , <i>Lagarostrobos</i> , <i>Manoao</i> , <i>Parasitaxus</i> , <i>Prumnopitys</i>)	<i>Prumnopitys limaniae</i> Pole <i>Prumnopitys</i> sp. Mt Somers (Pole, 1998) <i>Prumnopitys opihensis</i> Pole (Pole, 1997)	Paleocene	67 (55–98)	101 (73–135)
4. Podocarpaceae (Podocarpaceae, Araucariaceae)	<i>Mataia podocarpoides</i> (Ettingshausen) Townrow <i>Nothodacrium warrenii</i> Townrow <i>Rissikia</i> Townrow	Upper Triassic–Jurassic	197 (178–257)	193 (177–223)

record was accommodated by providing a parametric (log-normal) prior probability distribution for the age of the node. The details of the fossil calibration priors are presented in Table 1.3 and are illustrated in Figure 1.3. In each instance, the estimated fossil age was used to define the zero offset of the lognormal calibration prior, thereby imposing a minimum age constraint approximating the fossil age on the relevant stem node. In addition to the above constraints, an upper age constraint of 300 MYA was placed upon the age of the root. Although several extant lineages have been associated with microfossils extending back before the earliest known macrofossils (see Morley, this volume), we preferred the macrofossil evidence because of its greater complexity of characters. This allows greater confidence in the assignment of fossil material to extant lineages as the problems of homoplasy in the fossil record tend to increase with clade age (Wagner, 2000), which can readily mislead inferences when there are few characters for comparison (e.g., Willyard et al., 2007). Note that our calibration approach does not rule out much older ages (i.e., consistent with the microfossil dates) a priori as the calibration prior includes dates approximately twice as old as the macrofossil age in the 95% confidence interval (Table 1.3). We expect, however, that a detailed assessment of the fossil record of the Podocarpaceae is needed to identify synapomorphies uniting fossil and extant taxa (e.g., Saquet et al., 2009), rather than postulated relationships based upon gross morphological similarity.

For the analyses in BEAST, a GTR + I + Γ model of sequence evolution was assumed with the substitution model parameters unlinked across data partitions. An uncorrelated lognormal model of rate variation among branches in the tree and a Yule prior on branch rates was also assumed a priori. Four independent MCMC runs, each of 5×10^6 steps, were performed and subsequently pooled (after excluding an appropriate burn-in fraction, as determined using Tracer version 1.4; Rambaut and Drummond, 2007) to derive the 95% highest posterior density of topology and parameter estimates. The topology presented in Figure 1.3 is the maximum clade credibility tree derived from the sample of 20,000 trees, with clade posterior probability and 95% highest posterior density (i.e., 95% of topologies sampled from the posterior have values within this range) of divergence times indicated. As with the nonclock analyses, the genera and most of the deeper internal branches are strongly statistically supported. Furthermore, the relationships inferred among lineages are generally consistent among the clock and nonclock phylogenetic analyses (compare Figures 1.2 and 1.3).

ANALYSES OF DIVERSITY

TEMPORAL PATTERNS OF DIVERSITY

Although the family appears to be of ancient origin (mid-Mesozoic, 95% highest posterior density 177–223 MYA), the molecular dating analyses suggest that the majority of extant genera have arisen relatively recently (Upper Cretaceous to Cenozoic; Figure 1.3), whereas the extant crown groups of these genera are estimated to have diversified from predominantly the mid- to late Cenozoic. In Figure 1.4, the number of species in the phylogeny from the origination of the clade to the present (log scale) is plotted against the relative timing of inferred speciations (proportion of time since origination of the clade). This lineages-through-time plot shows a gradual increase in the rate of lineage accumulation and then an upturn at approximately 40 MYA, reflecting the estimated recent timing of the origination of most extant lineages.

Lineages-through-time plots have been widely used to infer macroevolutionary patterns; for instance, comparison of the data to a Yule (or pure birth) speciation model can be used to make inferences regarding the tempo of evolution (e.g., Harmon et al., 2003; Ricklefs, 2007; Rabosky and Lovette, 2008). Under a Yule model, there is an instantaneous rate of per lineage speciation and no extinction, giving an exponential increase in the number of lineages through time. Significant departures from this null model are indicative of temporal variation in the diversification rate (i.e., the per lineage rate of speciation and/or extinction; Harmon et al., 2003).

In Figure 1.5, the expectation under a Yule model was generated by connecting the point representing the first node in the phylogeny with the point representing the number of extant podocarp taxa (173) on the log-linear lineages-through-time plot. This resulting straight line provides the null hypothesis of exponential growth of lineages. To provide a confidence interval on the expectation of exponential growth, 100 phylogenies were simulated under a Yule model, each giving rise to 173 extant lineages. Clearly, the podocarp data show significant departure from the null model of exponential diversification, the comparison being consistent with the hypothesis that diversification rates in the Podocarpaceae have increased toward the present. However, there are other plausible hypotheses that can be assessed using more complex models of diversification.

In Figure 1.6, the lineages-through-time plot is compared with a constant birth-death model, which includes

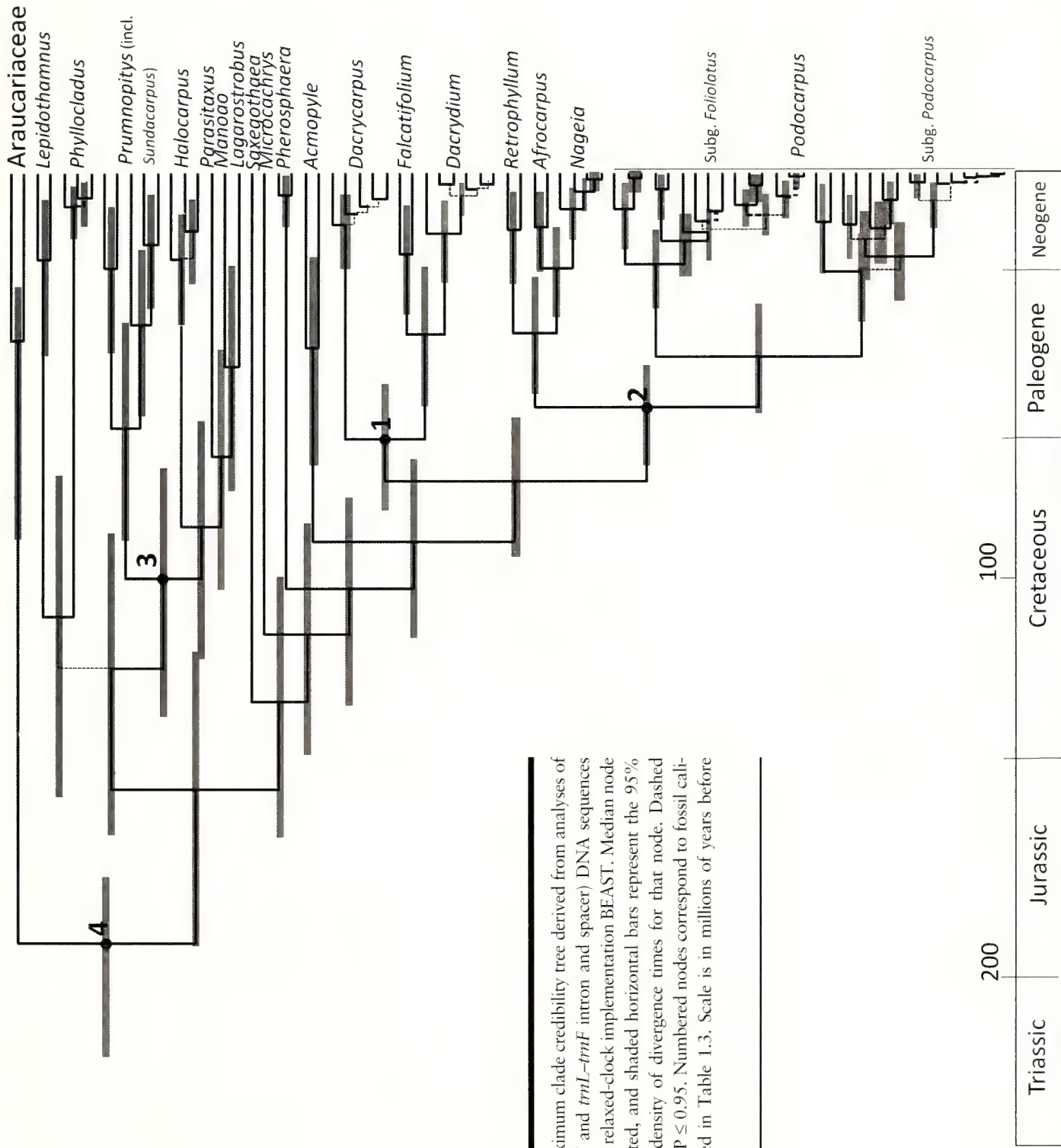


FIGURE 1.3. Maximum clade credibility tree derived from analyses of chloroplast (*matK* and *trnL-trnF* intron and spacer) DNA sequences using the Bayesian relaxed-clock implementation BEAST. Median node heights are indicated, and shaded horizontal bars represent the 95% highest posterior density of divergence times for that node. Dashed branches have a $PP \leq 0.95$. Numbered nodes correspond to fossil calibrations as detailed in Table 1.3. Scale is in millions of years before present.

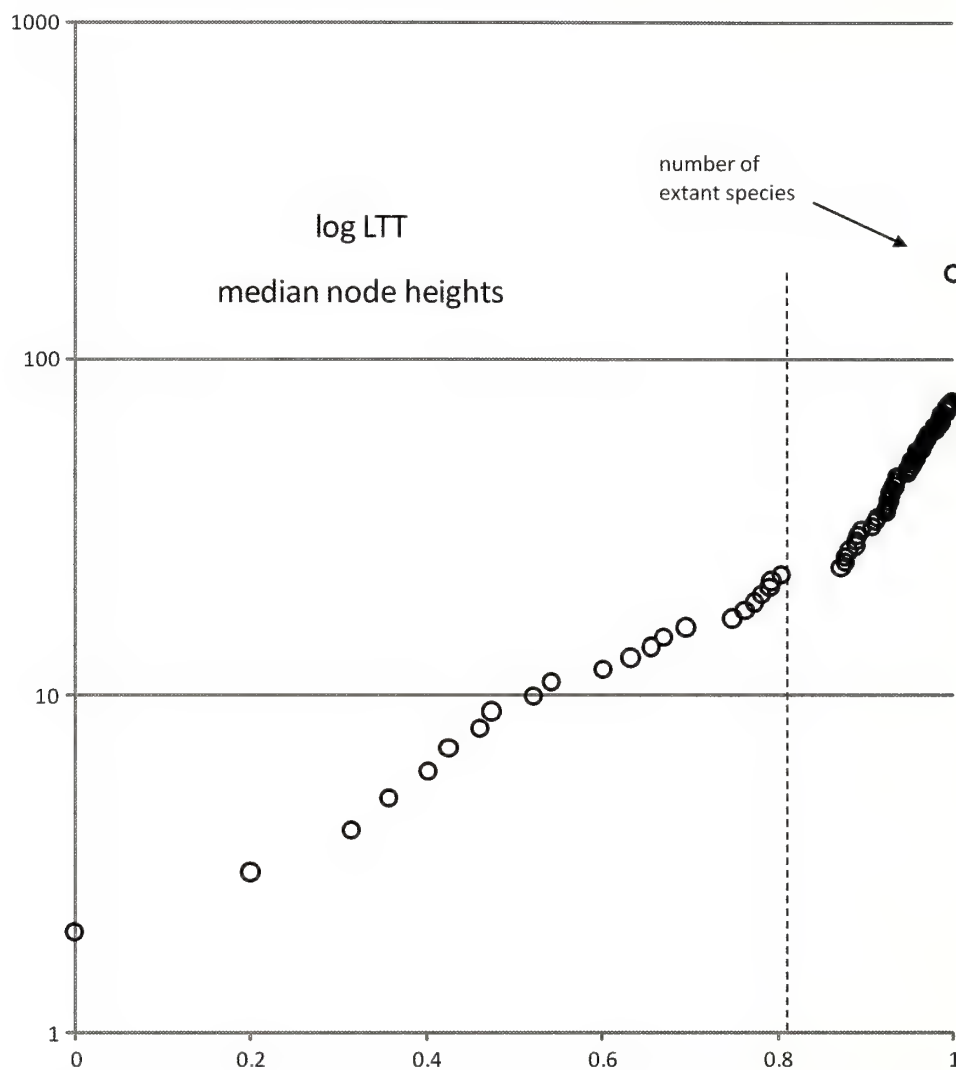


FIGURE 1.4. Lineages-through-time plot (log scale) for the Podocarpaceae based upon the relaxed-clock analyses of chloroplast data. Sampling is reasonably complete for approximately 80% of the time since origination (dashed vertical line).

an instantaneous rate of speciation and extinction. For the birth–death model, the extinction fraction was set to 0.95 (i.e., lineages have a 5% chance of survival to the present), and a 95% confidence interval was generated from 100 simulated birth–death topologies, as described above. As with the actual data, the simulated topologies show a sharp upturn toward the present and provide a close approximation to the data across the full depth of the Podocarpaceae phylogeny. In this instance, the sharp upturn in the rate of lineage accumulation may be ascribed to the “pull of the present” (Nee et al., 1994). That is, at a high relative extinction rate, the probability of a lineage persisting into the present decreases with the age of the

lineage, and therefore, recently evolved lineages are more likely to be observed in studies using only extant taxa. Recent simulation studies demonstrate that a similar upturn in lineages-through-time plots can also be generated under models with large declines in diversification rate, when the decline is mediated by a temporally increasing extinction rate (Rabosky and Lovette, 2008). Failure to consider extinction can lead to potentially spurious inferences of evolutionary tempo.

Rabosky (2008) provides a method by which a relative extinction rate can be approximated from phylogenetic data, which is implemented in the LASER package (Rabosky, 2006) for the R programming language. This

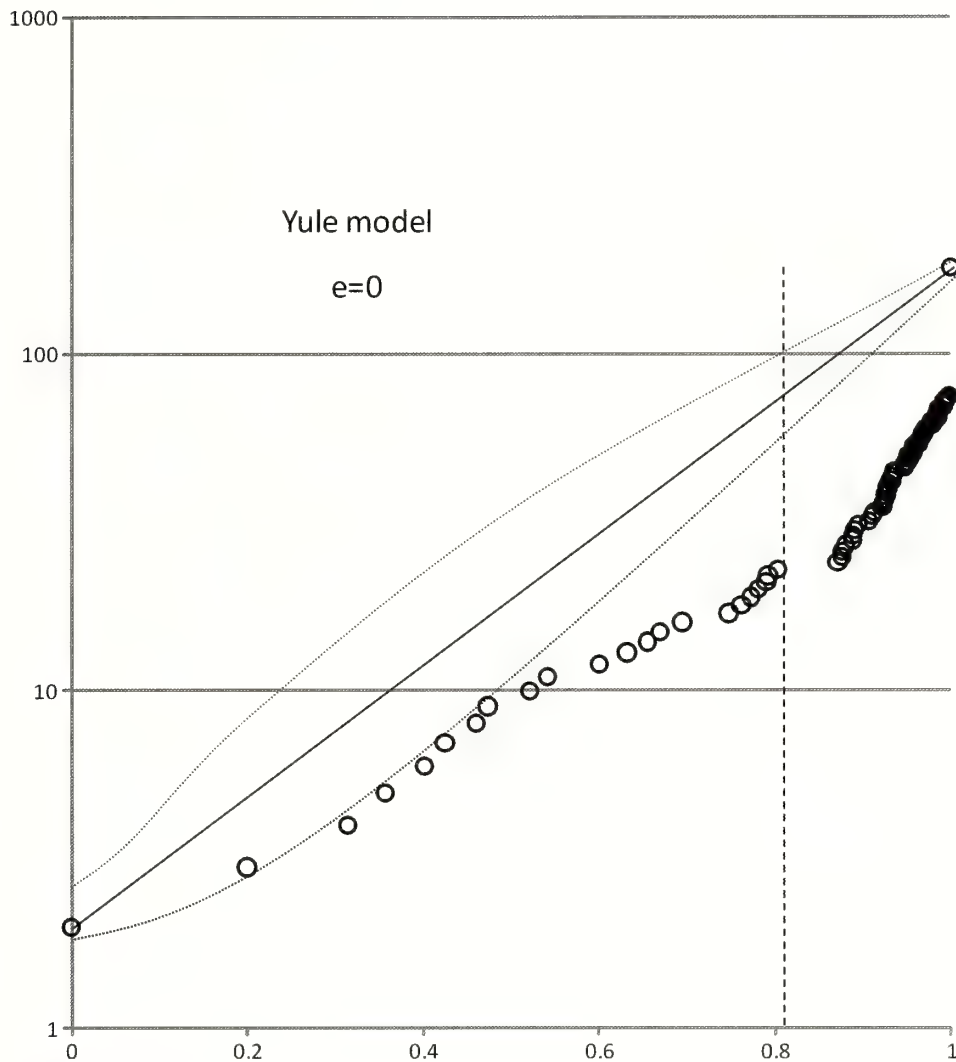


FIGURE 1.5. Lineages-through-time plot (log scale) for the Podocarpaceae compared to the expectation of exponential growth of lineages (Yule model; solid line). A 95% confidence interval on this expectation (dashed lines) was generated from 100 phylogenies simulated under a Yule model, each giving rise to 173 extant species.

method uses (ultrametric) branch length estimates and standing diversity estimates of terminal taxa to derive a maximum likelihood estimate of diversification rate, which varies with the relative extinction fraction (e). The likelihood surface can be visualized across the range of values of e to determine the value that returns the maximum likelihood estimate of diversification rate. For the podocarp data, this analysis was performed on an ultrametric topology (median node heights estimated from the relaxed-clock analyses, above) sampled to generic level by pruning all but one representative per genus, with generic species richness estimates assigned to the terminals according to Farjon

(1998) (see Figure 1.8). Figure 1.7 plots the likelihood surface for relative extinction fractions ranging from zero (no extinction) to 0.99 (99% of lineages go extinct) and suggests that (given the model) a relative extinction rate somewhat in excess of 0.9 (i.e., lineages have a <10% chance of surviving to the present) provides a reasonable approximation for these data. Although there are no direct estimates of an extinction rate for the Podocarpaceae derived from fossils, the inference of a high relative extinction rate seems reasonable in light of the levels of Cenozoic diversity of the Podocarpaceae in the Southern Hemisphere fossil record (Hill and Brodribb, 1999).

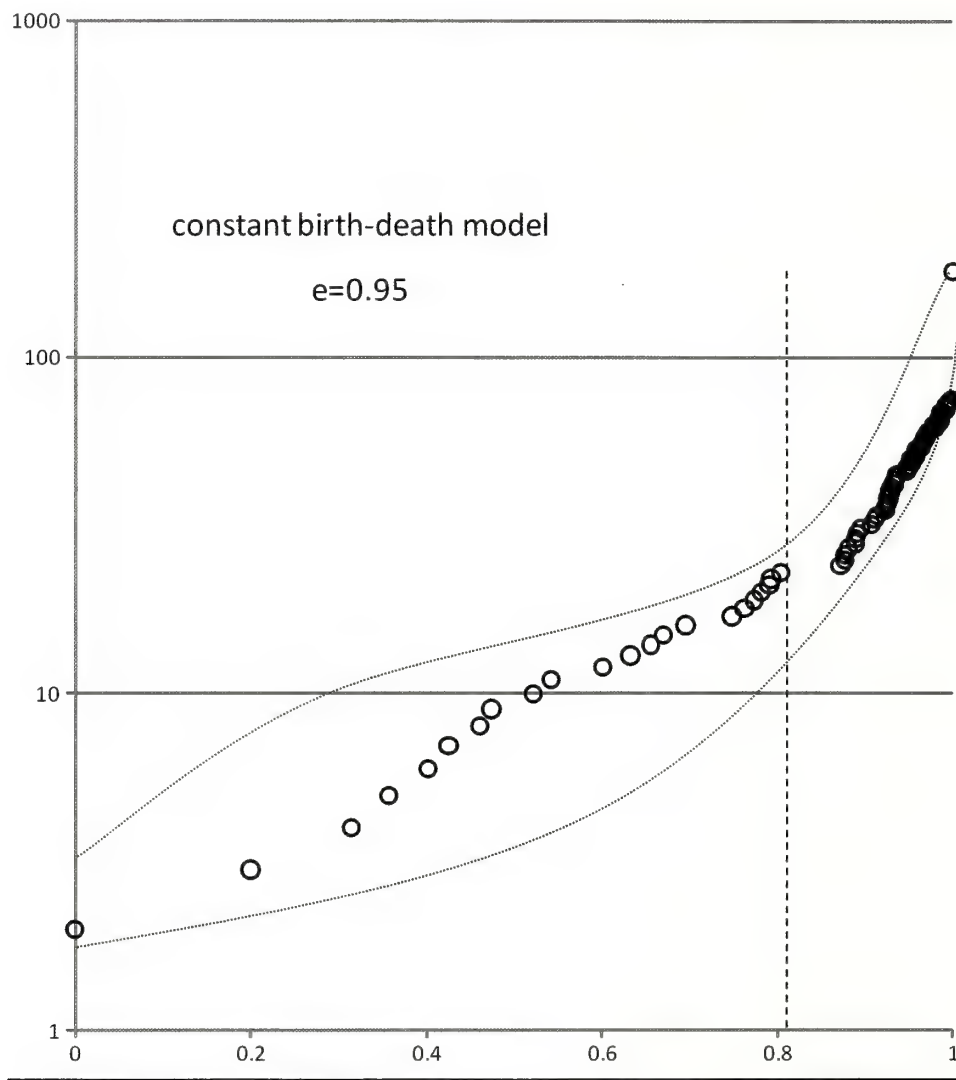


FIGURE 1.6. Lineages-through-time plot (log scale) for the Podocarpaceae compared to the expectation under a constant birth-death speciation model. The dashed lines represent a 95% confidence interval generated from 100 phylogenies simulated under a time-homogeneous extinction rate of 0.95.

SHIFTS IN DIVERSIFICATION RATE

The above estimate assumes that the podocarp phylogeny was generated under a constant rate of lineage diversification, an assumption that can be tested by contrasting the likelihood of a model that fits a homogeneous diversification rate to the data with one in which an ancestral diversification rate shifts at some point to a new diversification rate (Sanderson and Wojciechowski, 1996.; Rabosky et al., 2007). These analyses were performed in LASER, using the branch length and per genus diversities as above, and were repeated for 100 topologies sampled

from the 95% highest posterior density of the BEAST runs to assess the robustness of the conclusion to variations in topology and branch length estimates. In the first instance, the relative extinction rate was set to 0.95, but subsequent analyses were performed using $e = 0$ to test that the conclusions were robust to the model assumptions. For both relative extinction rates and all sampled topologies, comparison of standing diversities with those expected under a uniform diversification rate rejects the null hypothesis of a homogeneous diversification rate for the Podocarpaceae ($p < 1 \times 10^{-5}$, $e = 0.95$). That is, the observed levels of diversity among the podocarpaceous lineages are better

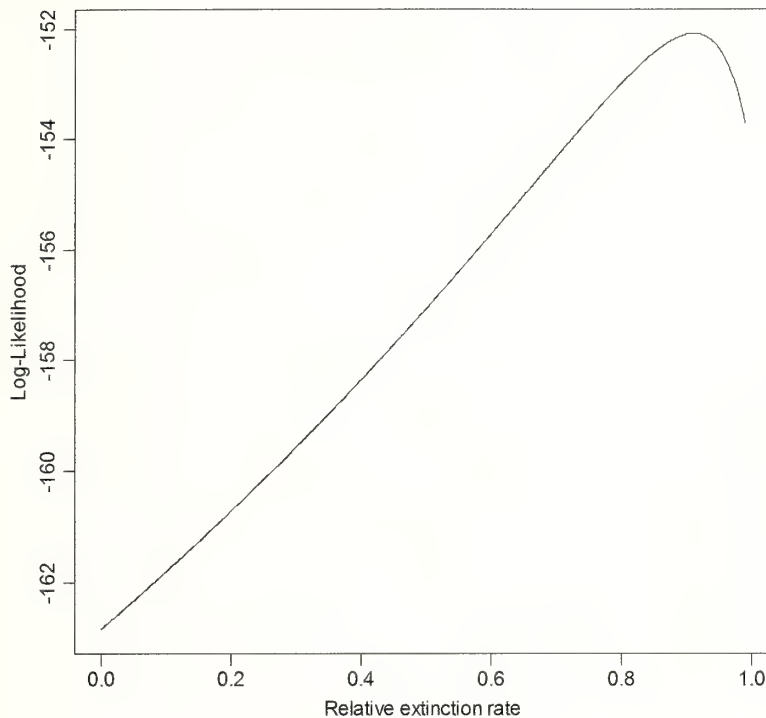


FIGURE 1.7. The likelihood of diversification rate estimates plotted against the relative extinction fraction under a model that assumes a homogenous diversification rate that varies with the extinction fraction. Analyses performed in LASER (Rabosky, 2006) using branch length and species richness data as in Figure 1.8.

accounted for by a model in which diversification rates have increased or decreased significantly at some point in the evolution of family.

For the variable diversification rate model, the phylogenetic tree is sequentially split at each node, and a diversification rate is optimized onto each descendant lineage. The maximum likelihood diversification shift point is the node with the highest combined likelihood obtained by summing the lineage-specific likelihood estimates from each bipartite tree (Rabosky et al., 2007). For the podocarp data, the maximum likelihood shift point is located on the most recent common ancestor (MRCA) of the Dacrydioid and Podocarpoid clades (Figure 1.8). The extent of this shift ranges from an approximately threefold ($e = 0$) to an eightfold increase in diversification rate at $e = 0.95$. At $e = 0.95$, other nodes with a likelihood (L) approaching the inferred maximum likelihood shift include the immediate ancestor of the Podocarpoid–Dacrydioid clade and the successively deeper node ($\Delta L = 3.5$ and 1.9 , respectively, compared to the maximum likelihood shift point), the *Podocarpus* crown node ($\Delta L = 3.53$), and the MRCA of *Lepidothamnus*, *Phyllocladus*, and the Prumnopityoid clade ($\Delta L = 4.9$) (Figure 1.8). The latter is the largest diversification rate *decrease* inferred from these data. Among these, the two successive nodes immediately below the maximum likelihood shift point are perhaps a consequence of “trickle down,” that is, potentially

spurious inference of rate shifts stemming from the nested nature of phylogenetic data and the high diversity of immediately more nested nodes (Moore et al., 2004). Similarly, the Podocarpoid–Dacrydioid clade not only includes *Podocarpus* but also unites other, relatively species rich, clades (e.g., the Dacrydioid clade with 35 species) and has a likelihood score exceeding the immediately more nested nodes. The identified maximum likelihood shift point was robust to variations in the modeled extinction fraction.

TIMING AND CORRELATES OF SHIFTS IN DIVERSIFICATION RATE

A major event in the evolution of land plants was ecological radiation and taxonomic diversification of flowering plants, which is concomitantly associated with declining diversities among other plant groups, including conifers (e.g., Crane, 1987; Crane and Lidgard, 1989; McElwain et al., 2005). The major diversification of angiosperms is believed to have occurred in the mid- to Late Cretaceous (middle Albian to early Cenomanian, approximately 100–94 MYA); for instance, there is a dramatic increase in the representation of angiosperms in regional palynofloras (from approximately <5% to >40%) over a 40 million year period from the mid-Cretaceous, consistent with rapid radiation (Crane, 1987). Although the timing is debated, angiosperm-dominated megathermal

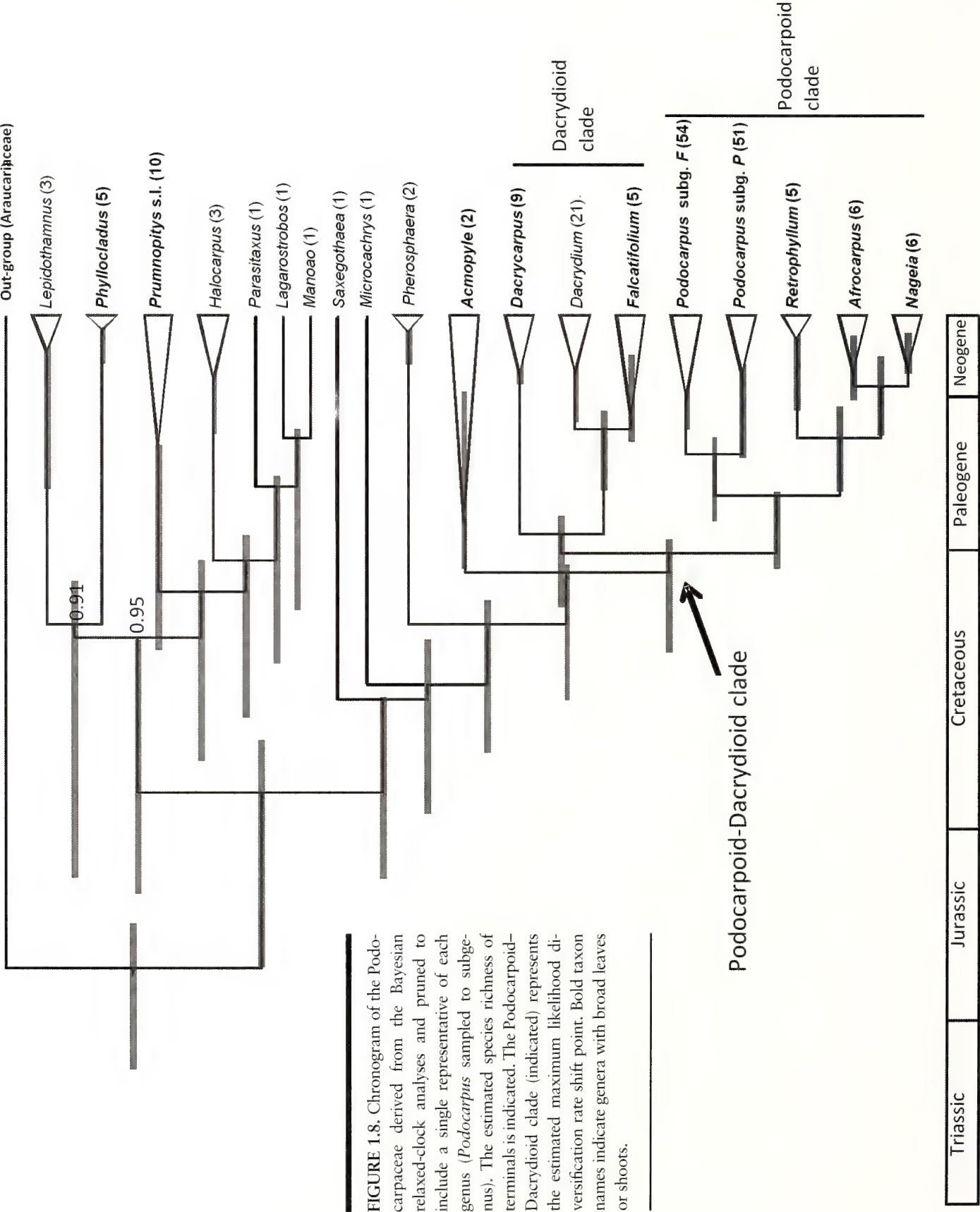


FIGURE 1.8. Chronogram of the Podocarpaceae derived from the Bayesian relaxed-clock analyses and pruned to include a single representative of each genus (*Podocarpus* sampled to subgenus). The estimated species richness of terminals is indicated. The Podocarpoid-Dacrydioid clade (indicated) represents the estimated maximum likelihood diversification rate shift point. Bold taxon names indicate genera with broad leaves or shoots.

forests appear to have expanded principally from the Albian (e.g., Davis et al., 2005) to the Cretaceous–Tertiary boundary (e.g., Morley, 2000). Interestingly, these dates accord with the inferred timing of the radiation of the Podocarpoideae–Dacrydioid clade (Figure 1.3), which on the strength of the evidence presented here, has experienced higher speciation and/or lower extinction rates relative to other podocarp lineages (Figure 1.8).

Among conifers, the podocarps are unusual in that an overwhelming majority of taxa are restricted to humid environments, including angiosperm-dominated forests extending into the tropics. Explanations for this pattern have been sought from comparative ecophysiology and from the paleobotanical and paleoclimatic data (reviewed by Hill and Brodribb, 1999; Brodribb and Hill, 2004; Brodribb, this volume). Briefly, the relative success of the Podocarpaceae in wet forests has been ascribed to morphological/physiological traits, such as leaf flattening, and life history characteristics, including the longevity of individuals, which are believed to facilitate regeneration of the podocarps among the dense shade of broad-leaved angiosperms (Brodribb and Hill, 1997, 2004; see also Brodribb and Feild, 2008). However, the physiological mechanism related to persistence of podocarps in wet forest environments appears to be associated negatively with drought tolerance (Brodribb and Hill, 1998, 2004; Hill and Brodribb, 1999), and the demise of several Podocarpaceae genera in Australia has been linked to decreasing rainfall, increasingly seasonal rainfall regimes, and increased fire frequency and intensity through the Cenozoic (Hill and Brodribb, 1999; Brodribb and Hill, 2004).

The Podocarpoideae–Dacrydioid clade comprises a predominance of taxa with broad leaves and shoots (*Afrocarpus*, most *Dacrycarpus* spp., *Falcatifolium*, *Nageia*, *Podocarpus*, *Retrophyllum*; Figure 1.8). As suggested elsewhere (e.g., Brodribb and Hill, 2004), leaf/shoot flattening among podocarps probably arose prior to the major expansion of flowering plants but subsequently contributed to the persistence of those lineages in low-light conditions beneath angiosperm-dominated canopies. Furthermore, the species included in the Podocarpoideae–Dacrydioid clade are, for the main part, concentrated in the tropics (cf. Kelch’s “tropical clade”; Kelch, 1997) and particularly the paleotropics. An exaptation to rainforests may have buffered those taxa from the extremes of historical climatic change relative to those experienced at higher latitudes (e.g., Dynesius and Jansson, 2000; Jansson and Davies, 2008) and facilitated northward expansion of “Gondwanan” lineages with the close proximity of the Australian and Sunda plates from the mid- to late Tertiary (Morley,

2003). Thus, a combination of ecophysiological adaptation/exaptation and the past and present distribution of suitable climates may have reduced the probability of extinction relative to imbricate-leaved lineages and facilitated range expansion and speciation.

CONTINGENCY, CONVERGENCE, AND KEY TRAITS

In light of the above results, the fact that some of the genera with broad shoots (*Acmopyle*, *Prumnopitys* sensu lato, and *Saxegothaea*; Figure 1.8) or phylloclades (*Phyllocladus*) have failed to radiate at a rate comparable to the Podocarpoideae–Dacrydioid clade requires explanation. Of these, *Acmopyle*, *Phyllocladus*, and *Prumnopitys* sensu lato have at least some representation within tropical regions. One possible interpretation is provided by historical contingency; that is, when the influence of a particular sort of character (for instance, on rates of speciation or extinction) is dependent on the proximity of other factors (de Queiroz, 2002). Fleshy fruits, for example, are associated with high rates of diversification among tropical rainforest understory angiosperms (Smith, 2001) but imperfectly in other contexts (Herrera, 1989). Certain putative “key traits” of angiosperms (vessels, reticulate venation, closed carpels) may have only achieved significance upon transition from the understory into high-light environments (Feild et al., 2004). Therefore, an imperfect correlation between a trait (or traits) and a particular mechanistic hypothesis to explain elevated diversification rates suggests the need to carefully consider other potentially significant associations (Donoghue, 2005). The long-term evolution of geographic range of the Podocarpaceae in the context of historical climatic/geological scenarios (e.g., Yesson and Culham, 2006; Moore and Donoghue, 2007) would be a fruitful avenue for further investigation given that it is “easier to move than evolve” (Donoghue, 2008:11551) and species–area effects can strongly influence past and present diversities (Jaramillo et al., 2006).

Furthermore, there can be different ways to construct an outwardly similar organ, and the various pathways can have different outcomes in terms of rates of lineage accumulation (Donoghue, 2005). In this context, the difference between parallel and convergent evolution may be significant. Given that leaf flattening is associated with several evolutionarily distant lineages in the Podocarpaceae (Figure 1.8), it is probable that similarities are convergent (i.e., constructed from different starting points). This appears to be the case for *Phyllocladus*, which develops broad phyllodes rather than true leaves, the latter being the otherwise general condition within the family. Similarly, the development

of leaflike shoots of small distichous, flattened leaves in several divergent lineages may represent an adaptation to catch light on the rainforest floor, but these shoots are lost when trees reach the canopy. Detailed studies of morphological variation, ideally including fossil taxa, would help distinguish parallel from convergent evolution in candidate traits and refine mechanistic hypotheses.

SUMMARY

We have presented a preliminary hypothesis of evolutionary relationships among the Podocarpaceae using molecular phylogenetic data. On this basis, we have incorporated fossil constraints to estimate molecular evolutionary rates and divergence times for lineages of the Podocarpaceae. In general, the molecular phylogeny is largely in agreement with conventionally (morphology) based classifications for the family, although relative to previous hypotheses there is a high level of confidence in most intergeneric relationships. However, there is weak support for the majority of relationships within genera, and we present evidence that the majority of species are of recent evolutionary origin. Although this could be taken to indicate an upturn in diversification rates toward the present, a similar pattern could be inferred, for example, under a homogenous rate of speciation and a high but constant rate of extinction. Although extinction rates appear to have been high among members of the Podocarpaceae, a major shift in diversification rate is estimated to be of mid- to Late Cretaceous age, which could reflect a response, in terms of reduced extinction and/or increased speciation rates, to the radiation and expansion of angiosperm-dominated forests. Although further work is needed, the results of this study highlight the potential of molecular phylogenetic approaches to develop and test a range of hypotheses in the context of evolutionary biology and ecology.

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Dispersal and Paleoecology of Tropical Podocarps

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ABSTRACT. The paleoecology of tropical Podocarpaceae is reviewed for Africa and Southeast Asia. The family first appeared in the Triassic of Gondwana, after which it diversified through the Cretaceous and earliest Tertiary, and although some Northern Hemisphere Jurassic records are known, it has essentially remained a southern or southern-derived family until the present day. It seems to show a preference for areas of wet climate throughout its history. *Podocarpus* sensu lato dispersed into Southeast Asia during the late Eocene, and its present distribution is best explained by dispersal from India and possibly multiple long-distance dispersal events from Australia. *Dacrydium* reached Southeast Asia during the early Oligocene, presumably by island hopping, via the Ninety East Ridge and India and subsequently expanded its range to Japan during the middle Miocene climatic optimum. It is likely that the dispersal pathway was via low-altitude heath forests. *Dacrycarpus* and *Phyllocladus* dispersed into New Guinea as the island became established during the late Miocene and then island hopped to Borneo during the mid-Pliocene. *Dacrycarpus* subsequently reached Sumatra and the Malay Peninsula during the Pleistocene. In Africa, *Podocarpus* sensu lato was probably present in upland areas during the mid-Tertiary but dispersed by island hopping between montane areas to West Africa in the late Pliocene. In both Africa and Southeast Asia, the Podocarpaceae have clearly increased their range within the low latitudes following mid-Pliocene global climate deterioration and the Northern Hemisphere ice expansion.

INTRODUCTION

The Podocarpaceae is an essentially Southern Hemisphere family of conifers, centered initially in Gondwana, subsequently in Australasia and southernmost South America, and currently in Malesia. The earliest firmly accepted podocarp macrofossils are from the Triassic of Gondwana, including Madagascar (Townrow, 1967; Axsmith et al., 1998; Anderson et al., 2007), with numerous subsequent records from the Jurassic of Patagonia (Gnaedinger, 2007), Africa (Townrow, 1967), India (Rao, 1943, 1947, 1949; Vishnu-Mittre, 1959; Suthar and Sharma, 1987; Srivastava and Gularia, 2006), Australasia (Townrow, 1967;

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Hill, 1994), and Antarctica (Oecipa, 1998). Podocarps were prominent across the Gondwanan region, including Patagonia (Archangelsky and Del Fueyo, 1989) and Antarctica (e.g., Poole and Cantrill, 2006), throughout the Cretaceous period (e.g., Dettmann, 1994; Douglas, 1994; Hill, 1994), with most modern genera appearing during the Cretaceous (Dettmann, 1994), possibly related to the onset of wetter and warmer climatic conditions associated with the opening of the Southern Ocean. Despite their mainly Gondwanan distribution, there are also scattered podocarp records from Laurasia, which include *Scarburgia* from the Yorkshire Jurassic, described by Harris (1979) and with bi- and trisaccate pollen (Van Konijnenberg-van Cittert, 1971), and *Harrisiocarpus* from Poland (Reymanowna, 1987). There are also several Mesozoic records of *Nageia*-like leaves from East Asia (Krassilov, 1974; Kimura et al., 1988; Zhou, 1983), but since the Late Triassic, *Nageia*-like *Stalagma samara* Zhou from China has monocolpate pollen, which is unknown in Podocarpaceae. These may be from a different group of conifers that has independently evolved wide multiveined leaves, or they may reflect an extinct clade of early podocarps. Tertiary macrofossils attributed to *Podocarpus* from the middle Eocene of Europe (including England) are now, however, considered to belong to Pinaceae and the genus *Cathaysia* (Van Konijnenberg-van Cittert, personal communication). All Tertiary macrofossils from mid- and high-latitude localities are thus in the Southern Hemisphere. Most “*Podocarpidites*” pollen from the Laurasian Tertiary is unlikely to be related to the Podocarpaceae; these types are more likely to be from extinct Pinaceae, with pollen in which the typically finely reticulate sacchi (typically more coarsely reticulate in podocarps) are larger than the body. However, some pollen referred to *Podocarpus* from the Miocene of Alaska is very convincing (Reinink-Smith and Leopold, 1995) and may truly reflect the former extent of the genus.

This paper reviews the history and paleoecology of the Podocarpaceae in the old-world tropics, through the Cretaceous, Tertiary, and Quaternary periods, based mainly on the pollen record. There are numerous misconceptions regarding the occurrence of conifers in the low latitudes, including that they are on the decline (de Laubenfels, 1988), that they are remnants of a former mixed gymnosperm/angiosperm Cretaceous vegetation (Richards, 1996:18), and that lowland podocarps have “descended” from montane taxa (de Laubenfels, 1988). The fossil record allows judgments to be made on each of these issues.

There are currently 105 species of Podocarpaceae in 10 genera in Malesia (Enright and Jaffré, this volume) and possibly 17 in Africa in 2 genera (Adie and Lawes, this

volume). In Africa, all species of *Podocarpus* and *Afrocarpus* are montane, whereas in Malesia, podocarps have common representatives in both montane and lowland habitats. Montane-restricted Malesian genera are *Phyllocladus* (with a single species), *Falcatifolium* (five species), *Dacrycarpus* (eight species), and *Prumnopitys* (two species). Genera with both montane and lowland representatives are *Dacrydium* (20 species, of which about 4 are common in lowland habitats) and *Podocarpus* (56 species, of which about 10 are lowland taxa). All species of *Nageia* occur in the lowlands, although one ranges into the montane zone (based on de Laubenfels, 1988). Although lowland species may occur in low numbers in species-diverse mixed dipterocarp forests, they are primarily elements of localities with poor soil or drainage issues, such as in kerangas (heath forest), peat swamps, limestone, coastal forest on sand, and coastal bluffs (for further discussion, see Enright and Jaffré, this volume).

POLLEN TYPES IN THE PODOCARPACEAE

The pollen of Podocarpaceae are invariably mono-, bi-, or trisaccate, with a single exception: the monospecific genus *Saxegothaea* possesses inaperturate pollen, which prompted Erdtman (1965) to suggest that this genus should be transferred to the Araucariaceae and others to place it in its own family, Saxegotheaceae (Gaussen, 1973; Woltz, 1985). However, current opinion is in favor of the genus being retained in the Podocarpaceae (e.g., Mill and Stark-Schilling, 2009), and molecular evidence (Biffin et al., this volume) suggests that the genus is, indeed, within the Podocarpaceae, but in an isolated, near-basal position. Some Mesozoic macrofossil cones with in situ pollen variously attributed to the Podocarpaceae include *Rissikia* from the Jurassic of Australia, with bisaccate and striate-bisaccate pollen, as well as *Nothodacrium* from the Jurassic of Antarctica (Townrow, 1967) and *Apterocladus* from the Early Cretaceous of Patagonia (Archangelsky, 1966), both with “*Callialasporites*”-type pollen. Balme (1995) considered the latter two taxa to be araucarian and the former taxon (at least the male cone *Masculostrobus warrenii* ascribed to *Nothodacrium warrenii*) as a doubtful podocarp, based on its araucarian pollen. As noted above, *Stalagma samara* from the Late Triassic of China, attributed to Podocarpaceae by Zhou (1983), has monocolpate pollen and is therefore unlikely to be a podocarp.

It is noteworthy that the trisaccate condition is restricted to the Podocarpaceae (except for aberrant grains)

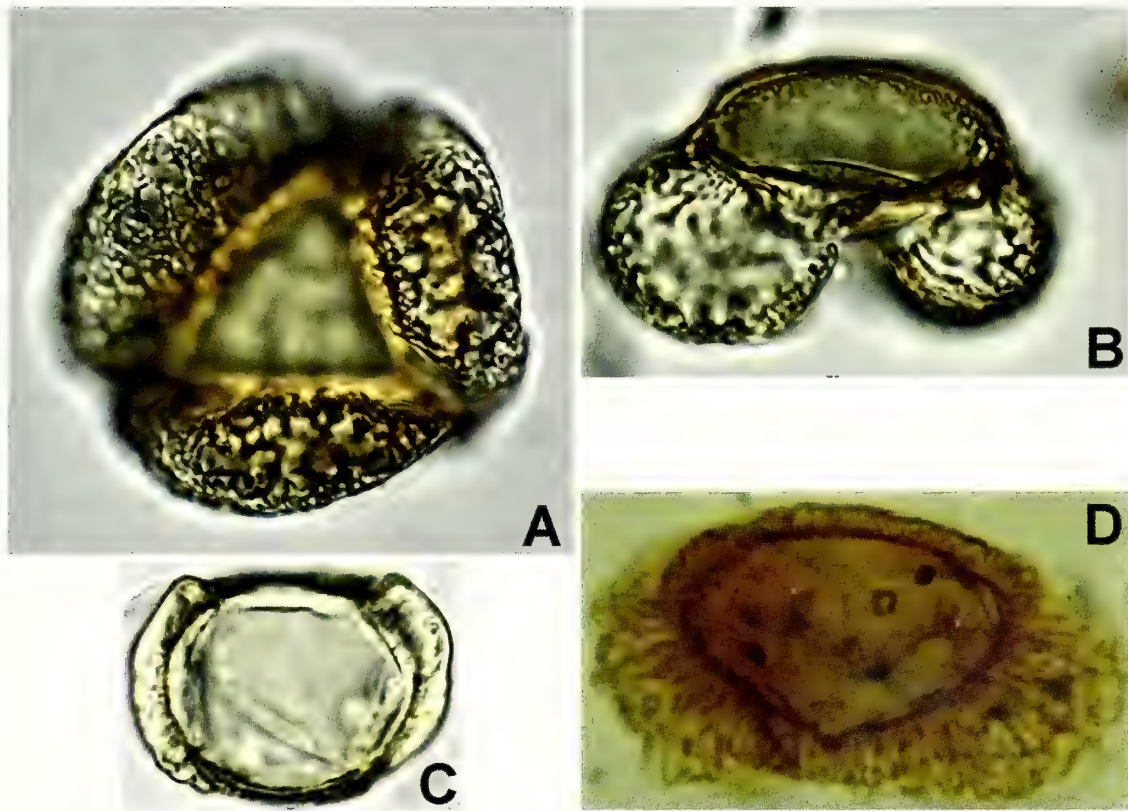


FIGURE 2.1. Pollen of the Podocarpaceae, showing (A) *Dacrycarpidites antarcticus* = *Dacrycarpus* pollen; (B) *Podocarpidites* sp., in *Podocarpus*, *Nageia*, *Prumnopitys*; (C) *Phyllocladites palaeogenicus*, in *Phyllocladus hypophyllus*; and (D) *Lygistepollenites florinii*, in most *Dacrydium* spp. Images A–C show modern pollen from *The Australian Pollen and Spore Atlas* (<http://apsa.anu.edu.au>); D is fossil pollen from Oligocene of Java (photo by Eko Budi Lelono).

and also seems to be near basal to the group, with a fossil record extending to the Middle (e.g., Van Konijnenberg-van Cittert, 1971; Suthar and Sharma, 1987) and Early Jurassic (de Jersey, 1971). The immediate ancestor to the Podocarpaceae should therefore yield a pollen type from which the simple trisaccate condition seen in *Trisaccites* (e.g., Baldoni and Taylor, 1982) could be readily derived.

The record of the Podocarpaceae from the low latitudes comes essentially from pollen (Figure 2.1). The dispersed pollen of the Podocarpaceae, both modern and fossil, were first described by Cookson (1947, 1953; Cookson and Pike, 1953a, 1953b, 1954), and modern pollen were subsequently described by Pocknall (1981). There is a fair correspondence between pollen types and the major genera, as summarized in Table 2.1. For genera that occur in the low-latitude Tertiary, *Dacrycarpus* has trisaccate pollen (Figure 2.1A), whereas *Phyllocladus* has bisaccate pollen with diminutive sacci (Figure 2.1C). The genus

TABLE 2.1. Podocarp pollen types from the Southeast Asian Tertiary. *Microcachrydites antarcticus* is only known from probable reworked specimens from New Guinea.

Taxon	Dispersed pollen type	Reference
<i>Podocarpus</i> sensu lato	<i>Podocarpidites</i> spp.	Cookson (1947)
<i>Dacrydium</i>	<i>Lygistepollenites florinii</i>	Stover and Partridge (1973)
<i>Dacrydium</i> <i>guillauminii</i>	<i>Dacrydium guillauminii</i> type	Erdtman (1965)
<i>Dacrycarpus</i>	<i>Dacrycarpidites antarcticus</i>	Cookson and Pike (1953a)
<i>Phyllocladus</i>	<i>Phyllocladites palaeogenicus</i>	Cookson and Pike (1954)
<i>Microcachrys</i>	<i>Microcachrydites antarcticus</i>	Cookson (1947)

Podocarpus is typically characterized by bisaccate pollen, in which the sacci are often larger than the body (Figure 2.1B). However, similar bisaccate pollen occurs in *Lepidothamnus laxifolius* (formerly placed in *Dacrydium*), and there are also some *Pinus* species with somewhat similar pollen, so records of bisaccate *Podocarpus*-type pollen or *Podocarpidites* species need not be conclusive evidence for the genus *Podocarpus*. Fossil pollen is typically referred to morphotaxa, as indicated in Figure 2.1 and Table 2.1.

Dacrydium, as considered by Farjon (1998), contains just two pollen types: the “typical” form has a strongly rugulate body (Figure 2.1D) and is placed in the fossil taxon *Lygistepollenites florinii*, whereas monosaccate pollen occurs in *Dacrydium guillauminii* from New Caledonia and is reminiscent of *Tsuga* pollen in the Pinaceae. With the placement by Farjon (1998) of the New Zealand *Dacrydium laxifolium* (with *Podocarpus*-like pollen) into *Lepidothamnus* and the Tasmanian *Dacrydium franklinii* (with *Phyllocladus*-like pollen) into *Lagarostrobos*, the taxonomic significance of *Dacrydium*-type pollen has now been elevated, and the ambiguity previously discussed by Pocknall (1981) has disappeared with taxonomic revision.

EARLY CRETACEOUS PODOCARPS

Fossil woods occur widely in the Early Cretaceous of Africa and Indochina. The African woods have been reviewed by Dupéron-Laudoueneix (1991) and Dupéron-Laudoueneix and Dupéron (1995), and several examples suggest possible affinity (never definite) with the Podocarpaceae, such as *Metapodocarpoxyton*, which is one of the commonest elements (e.g., Philippe et al., 2003). They occur together with woods attributed to the Araucariaceae and the extinct gymnosperm family Cheirolepidiaceae. A second genus generally attributed to the Podocarpaceae is *Protophylocladoxyton*, also present in the Early Cretaceous of Indochina. However, bisaccate pollen, which is ubiquitous in extant Podocarpaceae (with the exception of *Saxegothaea*, as noted above), is virtually absent from Early Cretaceous sediments of both regions (e.g., for the Ivory Coast and Senegal, see Jardine and Magloire, 1965; for Indochina, see Racey et al., 1994, and Racey and Goodall, 2009), which are characterized by abundant *Araucariacites* and *Classopollis* pollen (the latter derived from the extinct gymnosperm family Cheirolepidiaceae). Since the attribution of these woods to the Podocarpaceae is mostly questioned (e.g., Philippe et al., 2003), it seems unlikely that these genera are from the Podocarpaceae, because podocarpoid bisaccate pollen would be expected to

occur in the same- or equivalent-age sediments. However, the possibility needs to be considered that the woods are allied to *Saxegothaea*, which as noted above, has inaperturate, *Araucaria*-like pollen. Here, paleoclimate evidence helps to clarify the relationships. Lithological and palynological evidence indicates that the paleoclimate was warm and dry, and the absence of tree rings suggests aseasonality. Today, virtually all podocarps, including *Saxegothaea*, are essentially restricted to wet climates; this throws further doubt on the possible podocarpaceous affinity of the wood fossils. The ambiguity in attribution of many Mesozoic wood morphogenera to extant families has recently been emphasized by Philippe and Bamford (2008).

The only records of bisaccate pollen from the Early Cretaceous of equatorial Africa that may have affinity with the Podocarpaceae are specimens referred to the morphogenus *Alisporites* (a morphotaxon name previously used to mean bisaccate pollen compressed in polar view) from the Barremian and Aptian of Gabon (Doyle et al., 1977). These are small in size, fitting with the current size range of many *Podocarpus* species, and occur in assemblages overwhelmingly dominated by *Classopollis* and *Exesipollenites tumulus* (Cheirolepidiaceae). Similar forms occur in the stratigraphically equivalent succession in Brazil (Regali et al., 1975). The occurrences of *Alisporites* species characterize the “synrift” period of development of the early Atlantic Rift, when upwarping would have resulted in elevated regions marginal to the rift, as is the case today for the East African Rift. They become less common in the Aptian during the early postrift phase and are absent from the Albion onward (Figure 2.2). It is therefore possible that these bisaccates were derived from Podocarpaceae growing in upland settings along the proto-Atlantic upwarp, in the same manner as some Podocarpaceae today along the East African Rift Valley. They then disappeared from the region as the Atlantic Rift went through the postrift phase, during which period the uplands bordering the Mid-Atlantic Rift would have disappeared by a combination of erosion and subsidence.

The analysis by Muller (1968) from the Pedawan Formation is still the only significant study of Early Cretaceous palynofloras from Sundaland (southeastern Asia). The lower part of the formation is thought to be of early Albion to Aptian age and, as with similarly aged localities from Africa, yielded abundant *Exesipollenites tumulus*, *Classopollis* spp., and *Araucariacites* spp. and very rare bisaccates of probable affinity with Laurasian conifers (Morley, 2000). Similarly, the Early Cretaceous Khorat Group, widespread across Indochina, is dominated by *Classopollis* pollen with few bisaccates (Racey et al., 1994). It is

from the region at the end of the Cenomanian, concomitant with the mid-Cretaceous rise of angiosperms (Figure 2.3). Gymnosperms did retain a presence, with the diversification of the Gnetales, characterized by *Ephedripites* species and elater-bearing pollen, but with wetter climates from the Campanian onward, the elater-bearing group became extinct and ephedroids became much reduced. Through the later Late Cretaceous, Araucariacean pollen remained present in significant quantities, only to disappear entirely from the record at the Cretaceous–Tertiary boundary, after which time there are no records of conifer pollen in West African assemblages until the cooling phase of the late Neogene.

SOUTHEAST ASIA

The upper part of the Pedawan Formation in Sarawak, dated as Turonian by Muller (1968) but more likely of Santonian age (Morley, 1998), is dominated by *Araucariacites* species and lacks any bisaccate pollen. It thus has similarities to the African equatorial palynoflora.

INDIA AND NEW GUINEA

Podocarp pollen (both bisaccate and the trisaccate *Microcachrydites antarcticus*) virtually disappears from the Indian record during the transition from the Early to Late Cretaceous, previously emphasized by Morley (2000) and confirmed from recent petroleum industry records of Noon and Brenac (personal communication). Similarly, in New Guinea records of *M. antarcticus* are absent from the Late Cretaceous. However, *Podocarpidites* records continue to occur infrequently in the Late Cretaceous of India (e.g., Bakshi and Deb, 1981), and fossil wood referable to *Podocarpoxydon* has been recorded from the intertrappean beds (Trivedi and Srivastava, 1989; Srivastava and Gularia, 2006). In general, podocarps appear to have played little part in the Late Cretaceous vegetation either of equatorial Africa, India, or Southeast Asia, although with the limited coverage of the palynological record for this time period in some regions they could possibly have been present in any upland areas.

TERTIARY AND QUATERNARY

INDIA

Scattered *Podocarpidites* records continue into the Paleocene of India (e.g., Saxena, 1991; Prasad et al., 2009)

and can be locally common (V. Prasad, Birbal Sahni Institute, Lucknow, India, personal communication), although Kar (1985) considers that pollen from *Podocarpidites* species from the Paleocene Matanomadh Formation of Kutch (northwest India) are reworked from the Early Cretaceous. The identity of Indian Paleogene *Podocarpidites* with *Podocarpus* needs careful review; although some published illustrations (e.g., Prasad et al., 2009: fig. 5.12) could, indeed, be from *Podocarpus*, others (Prasad, personal communication) referred to the form genus *Podocarpidites* are larger than any known Podocarpaceae, and their affinity with *Podocarpus* sensu lato (s.l.) is thus questionable. It therefore seems that *Podocarpus* s.l. was a sporadic element of Indian early Tertiary vegetation. It was an element of vegetation on islands of the Ninety East Ridge in the Indian Ocean during the Paleocene and Oligocene (Kemp and Harris, 1975).

SOUTHEAST ASIA

The Paleocene palynological record for Southeast Asia is very poor. The Kayan Formation in Sarawak (see Figure 2.4), interpreted to be mainly Late Cretaceous by Muller (1968), is most likely of Paleocene age. This succession is characterized by a low-diversity assemblage with the bisaccates *Alisporites similis* and *Rugubivesiculites redus*, which are probably derived from Laurasian conifers rather than podocarps (Morley, 2000). Further, Paleocene assemblages from the Pre-Ngimbang Formation from the East Java Sea region (R. J. Morley, unpublished data) lack any bisaccates, as do assemblages from the early Eocene Waripi Formation of New Guinea.

The palynofloras noted above are all relatively low diversity assemblages, and none can be envisaged to really “sample” the flora of each period sufficiently to confidently judge that bisaccate-pollen-producing plants were definitely absent from the regional vegetation. This is not the case for the middle Eocene Nanggulan Formation of Central Java, where a study by Lelono (2000) exhaustively recorded the palynoflora, describing over 300 morphotypes without any records of bisaccate pollen during this period of high global temperatures (Zachos et al., 2001). The pattern thus parallels that in West Africa, where intensive studies for the period following the Cretaceous–Tertiary boundary event consistently demonstrate the absence of conifer pollen. It thus appears that the Cretaceous–Tertiary boundary bolide impact exterminated conifers from the lowland paleotropics, with the possible exception of the Indian subcontinent. Subsequent occurrences of tropical conifers in Southeast Asia and Africa are therefore likely

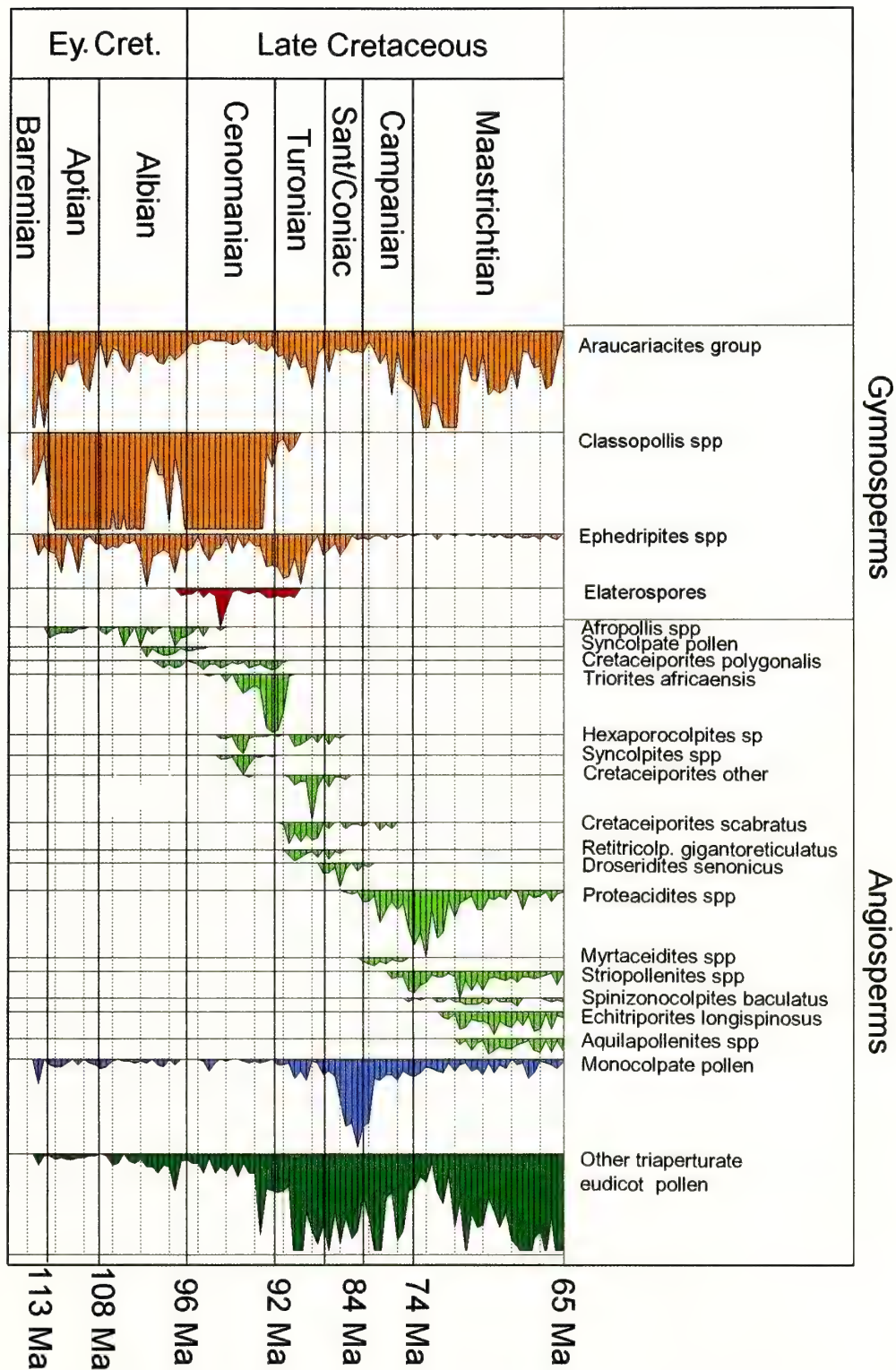


FIGURE 2.3. Occurrence of gymnosperm and angiosperm pollen in the Cretaceous of West Africa (Senegal and Ivory Coast) from Morley (2000), extracted from Jardine and Magloire (1965).

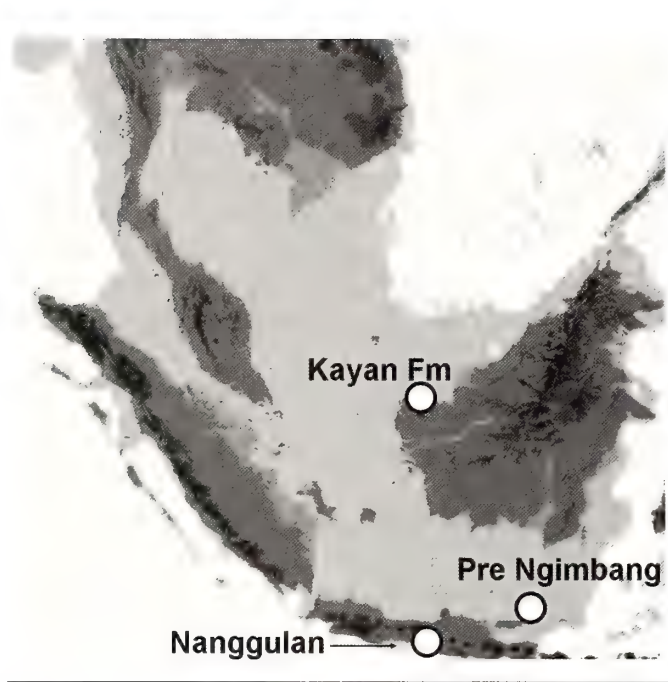


FIGURE 2.4. Paleocene and Eocene localities mentioned in the text.

to be due to immigration with dispersal via land bridges, filter routes, or via long-distance dispersal events.

Podocarpus *Sensu Lato*

Podocarpus-type pollen has a very long history in Australasia (Dettmann, 1994), extending throughout the Cretaceous. *Podocarpus* macrofossils have also been reported from the Paleocene of Patagonia (South America), with multiple species, together with *Retrophyllum* (Wilf et al., 2003; Iglesias et al., 2007).

In contrast, the first record of *Podocarpus*-type pollen from the Southeast Asian region is from the late Eocene section of the Nanggulan Formation in Central Java (Lelono, 2000). *Podocarp* pollen gradually appeared during the middle to late Eocene transition (Figure 2.5). The specimens are all small bisaccates typical of *Podocarpus* s.l., with a comparatively small body and coarsely infratreticulate sacci. The specimens are roughly divided into three morphotypes depending on overall shape, which may indicate more than one species. They are assumed to reflect *Podocarpus* growing in montane settings since (1) more than one species may be involved and (2) the specimens are more prominent in more open marine settings, where the supraregional pollen component will be more prominent. Immigration from India following late Eocene cooling is suspected, as previously suggested by Morley (2000).

From the early Oligocene onward, *Podocarpus*-type pollen occurs regularly in most stratigraphic intervals and in most areas, with regular records also from Vietnam, Taiwan, and China. There are also possible rare records from the Miocene of Siberia (Tomskeya, 1981) and Alaska (Reinink-Smith and Leopold, 2005), suggesting that *Podocarpus* may have ranged further north around the Pacific rim during the Miocene climatic optimum.

It is difficult to draw specific conclusions from the occurrence of *Podocarpus* pollen in Southeast Asian younger Tertiary sediments. Pollen occurs regularly in most sections, but in low numbers, and generally shows little change in abundance with depth in stratigraphic sections. Consequently, few judgments can be made with respect to its ecological significance. The commonest *Podocarpus* pollen type is of small size and has a small body, reminiscent of the common coastal tree *P. polystachyus*. Where this type occurs regularly and without other *Podocarpus* morphotypes, the pollen is assumed to come from a similar species growing in a coastal habitat. However, *Podocarpus* pollen often shows increased diversity, with the *P. polystachyus* pollen type being accompanied by larger types, which may possess a larger body, as in *P. neriifolius*. In such instances, the pollen is suspected to have been derived from montane settings. There is little evidence from pollen studies of peats, coals, or other organic-rich sediments to throw light on the former occurrences of *Podocarpus* that are currently associated with peat-forming settings, despite several *Podocarpus* species occurring today on peat swamps.

A good example suggesting derivation of *Podocarpus* pollen from montane forests is from the Parning hominin site near Mojokerto in East Java (R. J. Morley, unpublished data), which is of latest Pliocene or earliest Pleistocene age (Huffman, 2001; Huffman and Zaim, 2003). At least three *Podocarpus* pollen types accompany regular *Dacrycarpus imbricatus* pollen in a setting without lowland forests because of a strongly seasonal lowland climate (but moist montane climate), and this occurrence is taken to reflect a well-developed montane forest growing on nearby volcanoes, in a setting analogous to the drier islands of Nusa Tenggara (Indonesia) today.

Following their initial dispersal into Southeast Asia, presumably as montane taxa, have *Podocarpus* s.l. species subsequently “descended into the lowlands” (sensu de Laubenfels, 1988), or have different *Podocarpus* groups independently dispersed into the region from other areas? Since the current genera *Podocarpus* sensu stricto, *Nageia*, and *Prumnopitys* all have distributions that extend not only from Australasia to Malesia but also

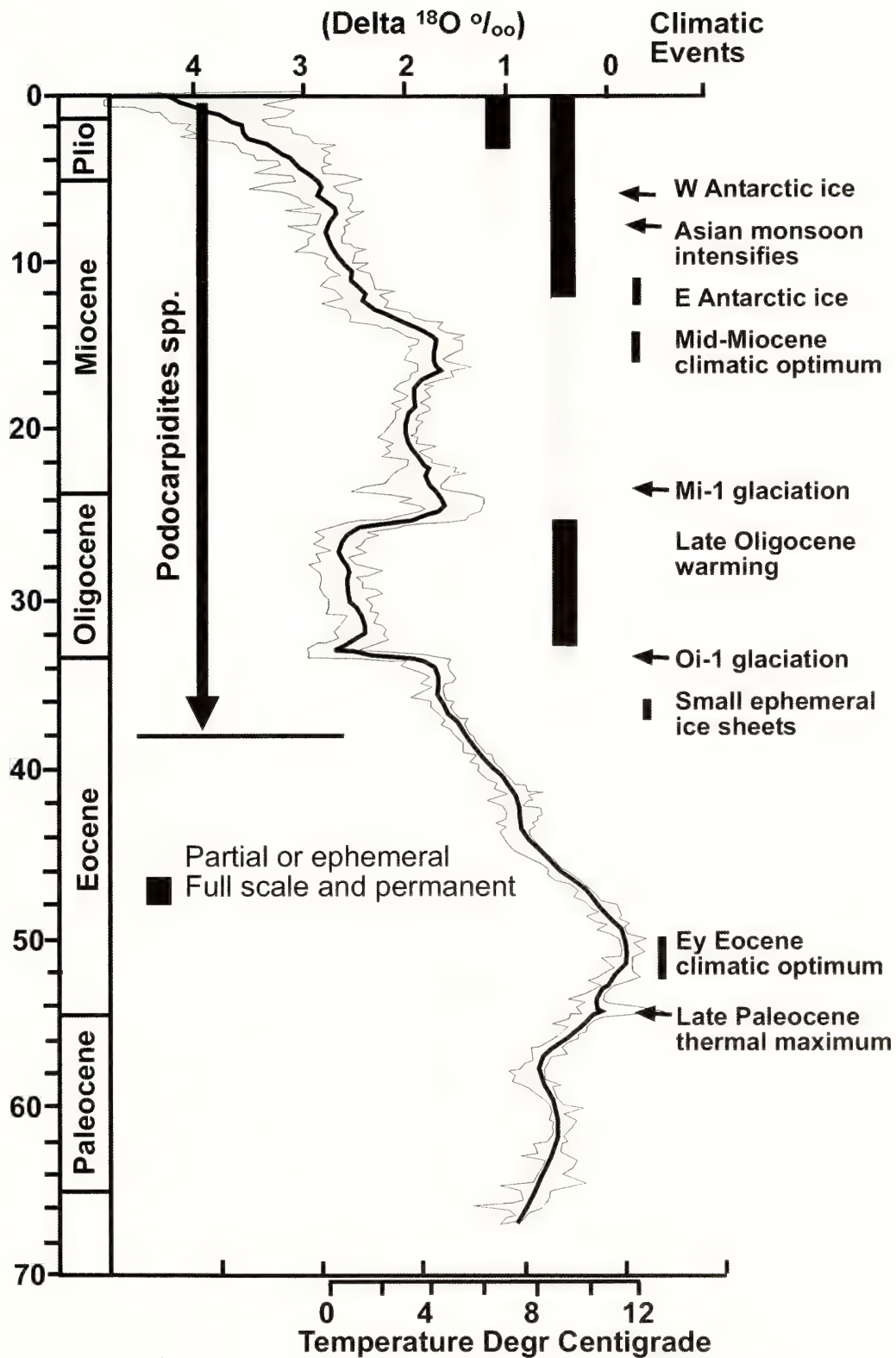


FIGURE 2.5. Appearance of *Podocarpus* pollen in Southeast Asia in relation to the trend of global climate change as indicated by oxygen isotope data of Zachos et al. (2001).

to South America (*Prumnopitys*, *Nageia*, *Podocarpus*), India (*Nageia*), and Africa (*Podocarpus*), it is likely that at least three or more dispersal events occurred to account for the Malesian populations of the Podocarpaceae producing the “*Podocarpidites*” pollen type. These events could have taken place at any time from the late Eocene onward, and thus the idea of “descent” is unlikely to apply since with lowland and upland taxa being from different genera, they are more likely attributable to different dispersal events.

Podocarpus during the Late Quaternary

Many *Podocarpus* species are prominent in montane forests, and there is a good record for *Podocarpus* from numerous late Quaternary lake and peat deposits occurring across the region. The general pattern shows that for montane sites, lower montane forests expanded in area during the Last Glacial Maximum as equatorial temperatures became reduced (Cannon et al., 2009). At the same time upper montane forest was less well represented than today but expanded to its current distribution during the postglacial period (Flenley, 1995). Southern conifers are common elements in both lower and upper montane forests, and *Podocarpus* species are elements of both of these habitats. The behavior of podocarps with changing temperatures will be discussed further below in the sections on *Dacrydium* and *Phyllocladus*.

Dacrydium

Dacrydium pollen is widespread throughout the Australian Tertiary, first appearing in the record in the Santonian stage of the Late Cretaceous (Dettmann, 1994). It is also reported from the late Oligocene/early Miocene of Patagonia (South America) by Barreda and Palazzesi (2007). *Dacrydium* pollen is distinctly absent from middle Eocene and older sediments of Southeast Asia. It was suggested by Morley (1998, 2000) that *Dacrydium* first appeared in the Sunda region in the Miocene following the onset of collision of the Australian and Asian plates, based on the sudden appearance of *Dacrydium* pollen in the latest part of the Talang Akar Formation (now dated as latest Oligocene) from the West Java Sea (Figure 2.6). This event also coincides approximately with a change from a seasonal to an ever-wet climate in that area. Recent studies in East Java by Lelono (2007) and Lelono and Morley (In press), however, suggest that *Dacrydium* may have a much earlier record, with common occurrences of *Dacrydium* pollen from the mid-Oligocene onward and regular occurrences

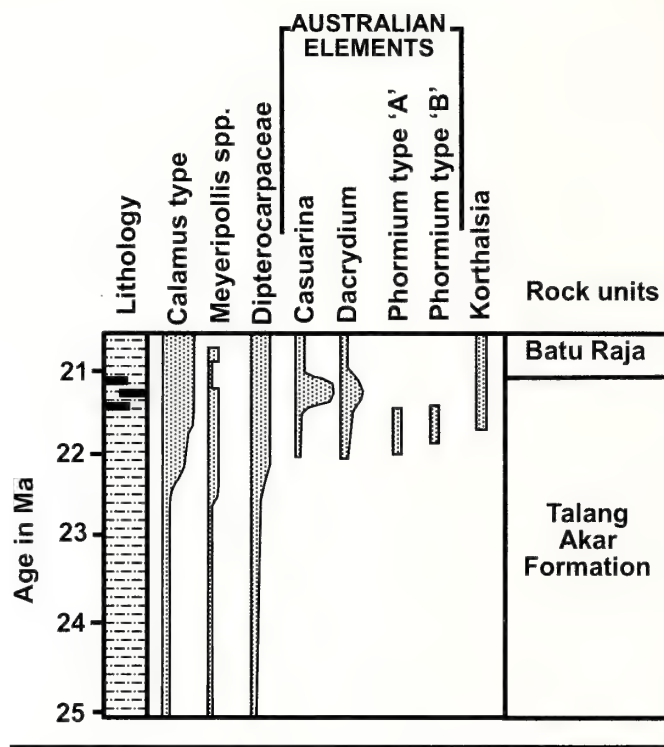


FIGURE 2.6. Appearance of Australian elements in the Tertiary of West Java (from Morley, 2000).

also through the early Oligocene. These data suggest that *Dacrydium* had established itself in the Sunda region by the beginning of the Oligocene. The very common occurrence of *Dacrydium* pollen suggests that it was growing in lowland habitats.

The earlier immigration of *Dacrydium* into the Sunda region raises questions as to its mode of dispersal and its ecology. During the early Oligocene there still would have been a wide ocean of perhaps 1,000 km between Sunda and Australia (Hall, 1998), so dispersal via a direct filter route from Australia is unlikely. For dispersal to have taken place via a land corridor, it is more likely to have arrived via India. Unpublished records from the Indian subcontinent by Noon and Brenac (personal communication) indicate that *Dacrydium* was already present there in the early Eocene (although now extinct). Since there are records of *Dacrydium* from the Paleocene and Oligocene of the Ninety East Ridge (Kemp and Harris, 1975), it is thought that *Dacrydium*, which is dispersed by birds, first dispersed into the Indian subcontinent, probably via island hopping, from Australasia via the Ninety East Ridge, prior to immigration into Southeast Asia during, or just prior to, the early Oligocene.

The absence of *Dacrydium* from the earlier Oligocene in the West Java region is probably attributable to climatic factors. West Java experienced a seasonally dry climate during the early Oligocene (Morley, 2000), which would not have been suitable for *Dacrydium*, whereas ever-wet climates were more persistent in the East Java region throughout the middle Eocene to Oligocene (Lelono and Morley, In press). The dispersal of *Dacrydium* into the Southeast Asian region approximately during the early Oligocene also explains the occurrence of scattered *Dacrydium* pollen in the late Oligocene of Natuna Sea sediments and its common occurrence through the late Oligocene of the Cuu Long Basin off the shore of Vietnam (R. J. Morley, unpublished data), as well as in the Oligocene of China (Sun et al., 1981). Following the Oligocene appearance of *Dacrydium* in the Sunda region, it spread quickly to China and reached as far north as Japan for a brief period during the mid-Miocene climatic maximum (Figure 2.7) about 16 MYA, where it was a member of the Daijima flora (Tanai, 1972) and also to Korea (Yamanoi, 1992).

Dacrydium, CASUARINACEAE, and Peat Swamps

Occurrences of common *Dacrydium* pollen from the Southeast Asian Cenozoic are almost invariably associated with common occurrences of *Casuarina*-type pollen (Casuarinaceae; *Casuarina* and *Gymnostoma* share the same pollen type). The two are also frequently associated with coals and lithologies rich in organic carbon, with examples occurring throughout the Miocene and Pliocene. Today, *Gymnostoma* and *Dacrydium* often occur in association in inland “kerapah”-type peat swamps and in kerangas vegetation (Brunig, 1974, 1990). One of the most well-known peat swamps with vegetation consisting mostly of *Gymnostoma nobilis* and *Dacrydium beccarii* var *subelatum* occurs at Lawas, Brunei (see photo in Whitmore, 1975:171). Termed an “anomalous” peat by Anderson (1964), the palynological succession of this peat was studied by in the early 1960s, although he only published a very rudimentary discussion of the succession (Muller, 1965). He passed the original results to the author in 1981, and

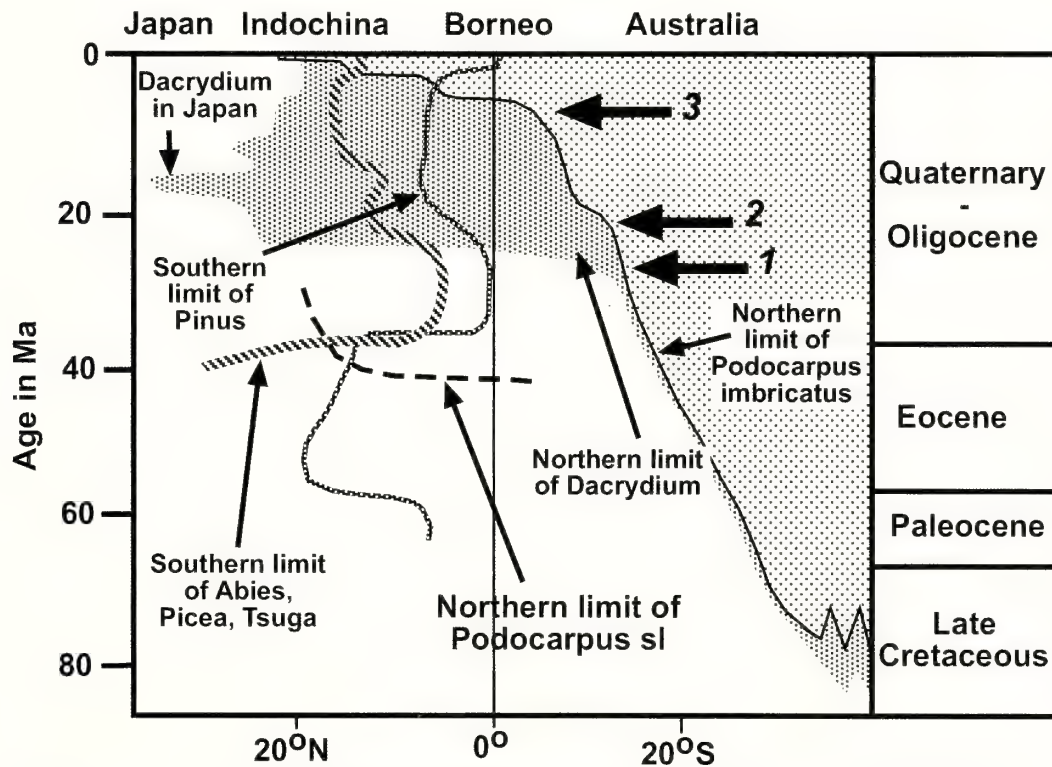


FIGURE 2.7. Dispersal of gymnosperms into Southeast Asia (from Morley, 2000), showing 1, collision of the Australian and Asian plates; 2, immigration of *Dacrydium* into New Guinea (approximate); 3, uplift in eastern Indonesia associated with the Sorong Fault.

Lawas, Brunei

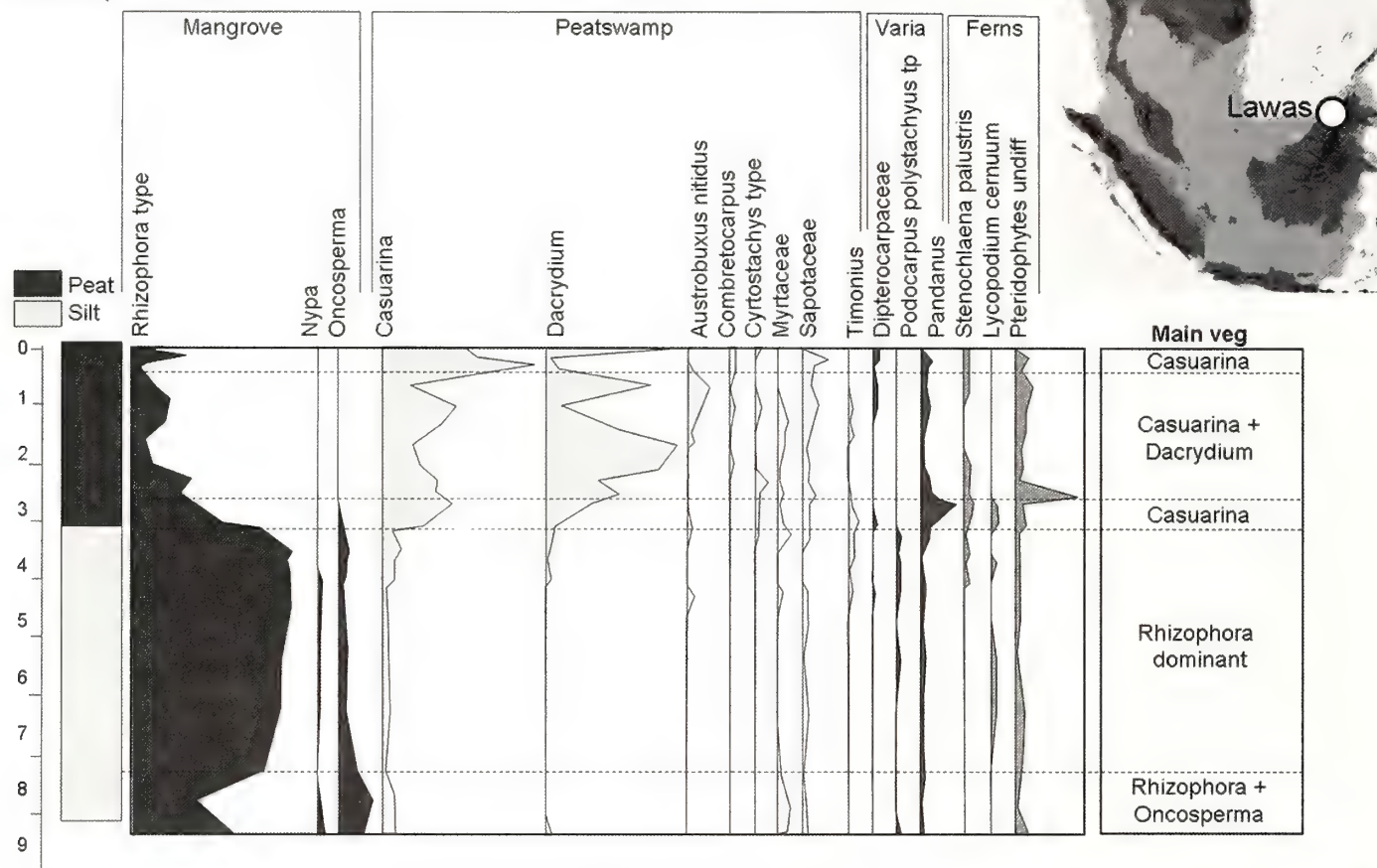


FIGURE 2.8. Palynological analysis of the Lawas peat swamp in Brunei. Analysis was performed by Jan Muller in 1963, but data are published here for the first time.

the data are presented here for the first time (Figure 2.8). The peat succession formed over a brackish *Rhizophora* (Rhizophoraceae) swamp with mangrove muds, which, in turn, overlay an interval with common *Oncosperma* (Arecaceae) pollen. Both *Dacrydium*- and *Casuarina*-type pollen are the most common elements of the palynoflora at the onset of peat formation, although *Dacrydium* seems to be more common in the middle part of the succession and *Casuarina* type more common in the upper part.

Dacrydium has been found to be a common element of watershed peats in South Kalimantan (Morley, 1981) and occurs commonly in kerapah peats in Sarawak (Brunig, 1974). However, it seems to be missing from basal peats (the domed peats that occur behind mangrove swamps on coastal plains). The Lawas peat seems to be the only one where *Dacrydium*/*Gymnostoma* peat forms over a substrate of mangrove mud.

Many coals from the Southeast Asian Cenozoic yield common *Dacrydium* and *Casuarina* pollen in association. This indicates that kerapah or watershed peats have been common elements of the landscape for more than 27 million years and thus represent one of the oldest plant associations from the region. The principal examples noted by the author are from (1) the Oligocene of East Java (Lelono and Morley, In press), (2) the late Oligocene Talang Akar Formation in West Java (Morley, 2000), and (3) the early Miocene of the Malay Basin in Seismic Group I (Morley and Shamsudin, 2006); and in laterally equivalent facies, (4) the strata of infilled incised valleys from the West Natuna Basin (R. J. Morley, unpublished data), (5) the middle Miocene coals from Southeast Kalimantan (Demchuk and Moore, 1988), and (6) the middle Miocene "Group E" coals from the Malay Basin (Shamsudin and Morley, 2006).

There is no real record of *Dacrydium* pollen that could be considered to be derived from montane environments during the Tertiary, although *Dacrydium* pollen has been found in many Quaternary montane sites. Whether *Dacrydium* descended into the lowlands or ascended into the mountains cannot be determined from the fossil record, although on the basis of the early arrival of clearly lowland *Dacrydium* in eastern Java, it is thought that ascent is more likely, but this theory needs to be tested by molecular studies.

Dacrycarpus

Dacrycarpus has a long history in Australia and New Zealand, first occurring in the late Paleocene (Martin, 1994), and in Patagonia (South America), first occurring in the early Eocene (Wilf, 2007). It dispersed to New Guinea (Figure 2.7) during the late Miocene (Khan, 1976), presumably as montane environments became established with uplift of the New Guinea mountains, well after the collision of the Australian and Asian plates. It then dispersed to the Philippines (van der Kaars, 1991) and on to Borneo during the mid-Pliocene, indicated by its appearance in marine sediments from the offshore Brunei region from that time and onward, initially reported by Muller (1966).

Dispersal probably occurred through a combination of global temperature decline and the creation of dispersal routes through uplift in the Philippine region. The appearance in northwest Borneo was within Nannofossil Zone NN15 between 3.4 and 4.04 MYA. Dispersal was probably by birds, and the dispersal route was through an island chain.

In Central Java, *Dacrycarpus* pollen was already present in Nannofossil Zone NN15, contemporaneous with its appearance in northwest Borneo; *Dacrycarpus* pollen is well represented in the late Pliocene to basal Pleistocene Java Man locality near Modjokerto, dated to approximately 1.8 MYA (R. J. Morley, unpublished data; Huffman, 2001). An area offshore from northwest Sarawak yields *Dacrycarpus* pollen from the basal Pleistocene to the present day. Sediments in this area are sourced from rivers that flowed from Sumatra across the Sunda Shelf, suggesting that dispersal to Sumatra did not take place until the early Pleistocene (Figure 2.9). In 2005 a petroleum exploration well drilled in the center of the Malay Basin yielded the first record of regular *Dacrycarpus* pollen in that area in basal Pleistocene sediments (palynological analyses on previous wells from this area were undertaken only on the early Pliocene and older succession). *Dacrycarpus* pollen also ranges into the earlier Pleistocene in Myanmar

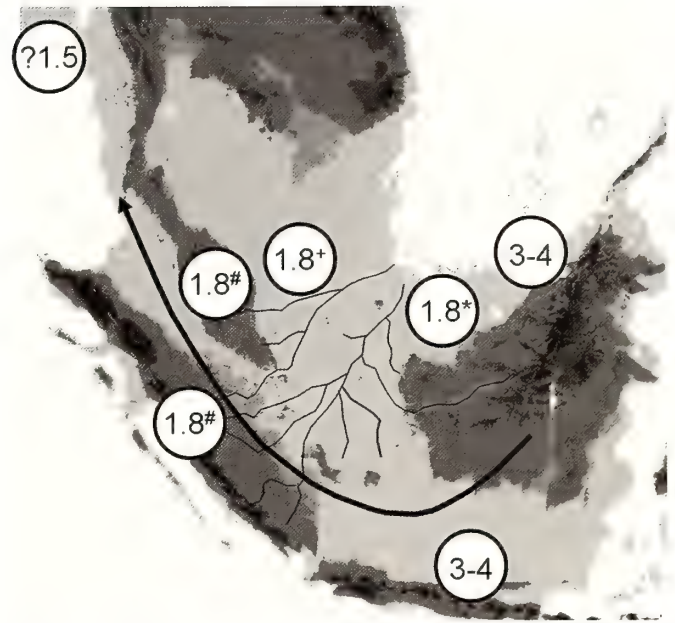


FIGURE 2.9. Dispersal of *Dacrycarpus imbricatus* across the Sunda region during the Pliocene and Pleistocene, based on pollen records. Dates are in millions of years. The positions of the Proto-Musi, Hari, Kampar, and Pahang rivers at the time of the Last Glacial Maximum (and older sea level low stands) are shown following Voris (2000). These rivers carried pollen that was deposited in the Malay Basin (+) and in deltas offshore from northwest Sarawak (*), dating dispersal from Borneo/Java to the mountains of Sumatra and the Malay Peninsula (#).

(Morley, 2000). It is likely that *Dacrycarpus* is still extending its range into Indochina.

In Southeast Asian montane regions, *Dacrycarpus* is very common in upper montane forest, which according to Flenley (1995), only forms during interglacial periods from taxa recruited from lower montane forest. During glacial periods, upper montane taxa retreat and find refuge in lower montane forest. Deep-sea cores from the Makassar Straits (Figure 2.10) indicate that in the last 30,000 years *Dacrycarpus* pollen is more common during the Holocene than during the last glacial. This occurrence is consistent with the Holocene expansion of upper montane forest in which *Dacrycarpus* was likely to have been a prominent member. However, *Lithocarpus* (Fagaceae) is considerably more common during the Last Glacial Maximum, consistent with the much greater expansion of lower montane forest during this time at the expense of lowland dipterocarp forest (Cannon et al., 2009). The Podocarpaceae do not appear to show increased representation in lowland forests during the Last Glacial

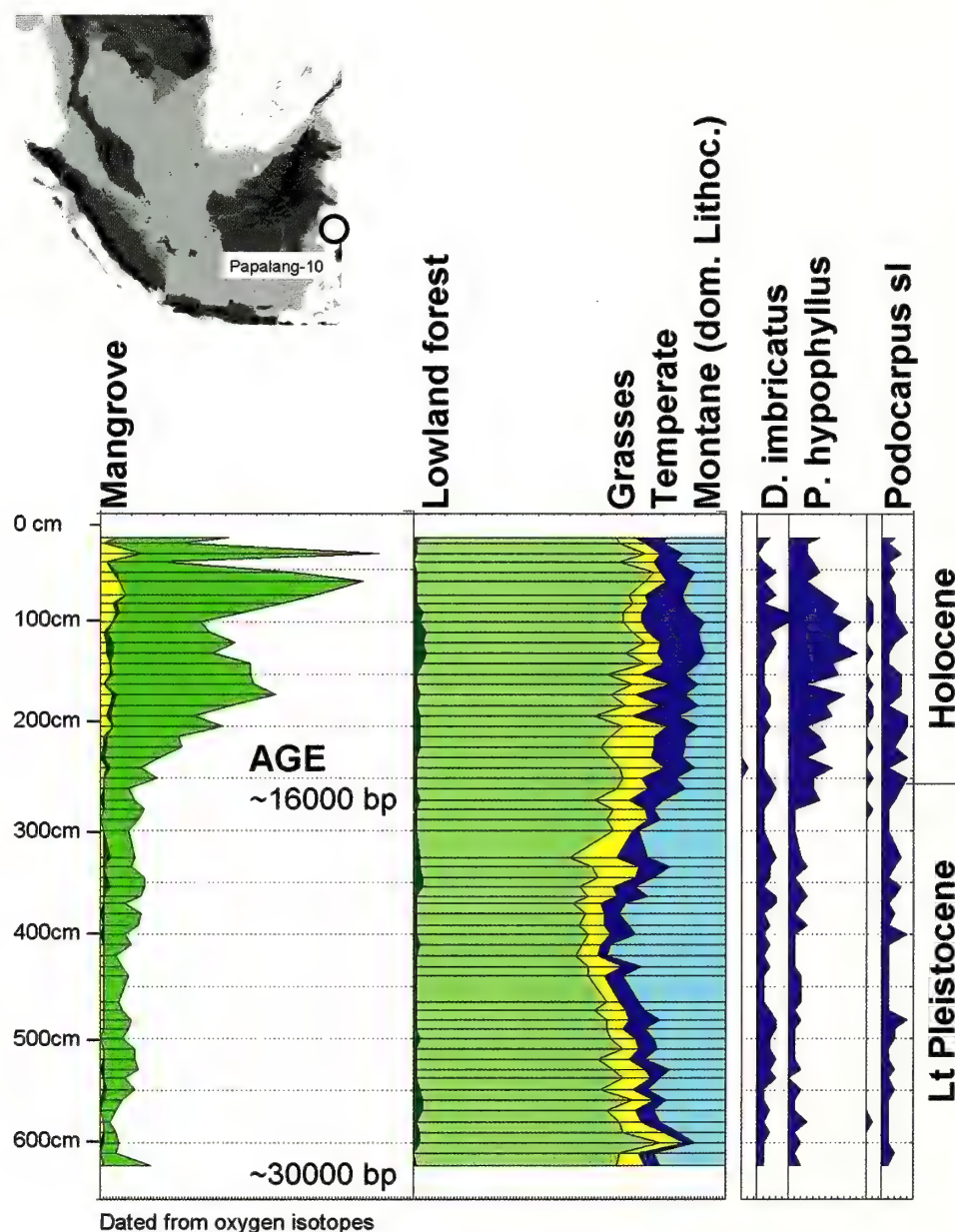


FIGURE 2.10. Summary palynological diagram showing occurrence of Podocarpaceae pollen from the Papalang-10 core, drilled in 2341 m of water at the base of the Mahakam Fan, Makassar Strait (Morley et al., 2004). The rare elements are *Alnus* (one specimen) and *Pinus*, probably carried by currents from the South China Sea.

Maximum, as has been demonstrated for the Amazon (Colinvaux et al., 1996).

Phyllocladus

Phyllocladus pollen has a long history in Australia, with the oldest records of bisaccate pollen from the

Paleocene (Martin, 1994). However, *Phyllocladus* pollen first appeared in northwestern Borneo just at the beginning of the Pleistocene about 1.9 MYA, with the parent plant presumably dispersing via New Guinea. It has no fossil record in the Sunda region outside the northwestern Borneo area, so it currently shows its maximum extension into the area. In late Quaternary sections, such

as in the Makassar Straits between Borneo and Sulawesi, it also shows increased abundance during the Holocene compared to the Last Glacial Maximum (Figure 2.10), which may also reflect the expansion of upper montane forest with climatic amelioration following the Last Glacial Maximum.

Microcachrys

Microcachrys-type pollen is found throughout the Tertiary of Australia (Martin, 1994) and has also been reported from the late Oligocene to early Miocene of Patagonia (South America) by Barreda and Palazzesi (2007). Kahn (1976) observed pollen of *Microcachrys* type in the New Guinea Pliocene. This distribution was used by Kershaw and McGlone (1995) to suggest that *Microcachrys* retracted its range during the Cenozoic. However, the *Microcachrys* specimens figured by Khan are dark colored and preserved poorly compared to the remainder of the assemblages and are most likely reworked elements from older sediments. *Microcachrydites antarcticus* is a regular component of palynomorph assemblages from the Bajocian (Middle Jurassic) to Early Cretaceous of Irian Jaya (Indonesia), and it is likely that the Pliocene specimens were reworked from Mesozoic sediments. *Microcachrys* was, however, reported from the Paleocene (ODP 214) and Oligocene (ODP 254) cores of the Ninety East Ridge by Kemp and Harris (1975).

AFRICA

In West Africa, conifer pollen is absent from the Cretaceous–Tertiary boundary until the mid-Pliocene, when *Podocarpus* pollen suddenly appeared about 2.7 MYA in the Niger Delta region (Knaap, 1972) and formed a useful stratigraphic marker. *Podocarpus* was likely to have been present in upland areas in East Africa through much of the Tertiary but dispersed to West Africa as global climates cooled during the late Pliocene. Maley et al. (1990) suggested that *Podocarpus* in West Africa dispersed from the East African highlands via upland areas in Angola (Figure 2.11). Poumot (1987) shows gymnosperm pollen occurring commonly throughout the late Miocene and Pliocene of the Niger Delta, but this was subsequently shown to be in error (Morley, 2000).

The time of dispersal into Africa is unknown, but *Podocarpus* pollen was present during the Early Cretaceous (see above), and it may have been present in upland areas away from the low latitudes throughout the whole of the Cenozoic. The timing of dispersal of podocarps into

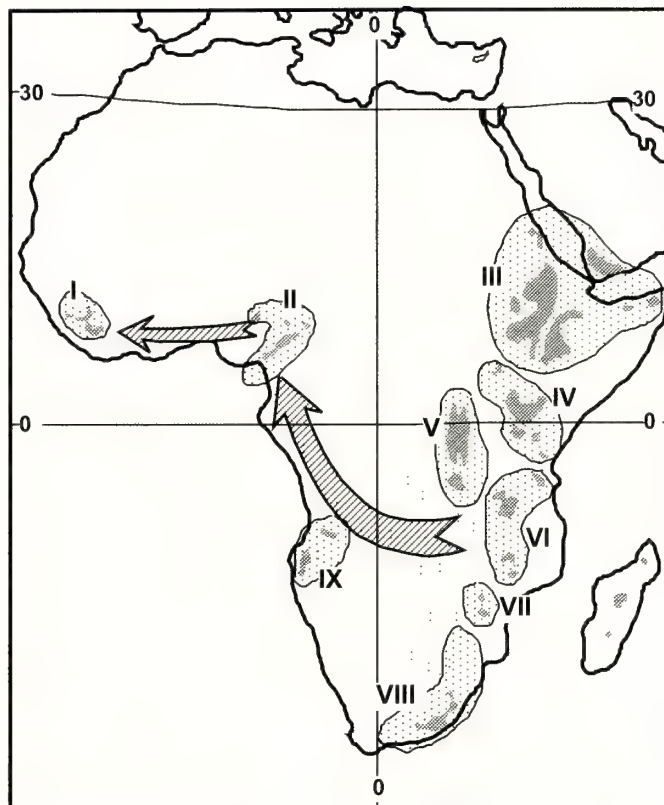


FIGURE 2.11. Dispersal path of *Podocarpus* into West Africa according to Maley et al. (1990). West African regional mountain systems as follows: (I) West African; (II) Cameroun-Jos; (III) Ethiopian; (IV) Imatonga-Kenya-Usambara; (V) Ruwenzori-Kivu; (VI) Uluguru-Mlange; (VII) Chimanimani; (VIII) Drakensberg; (IX) Angolan.

Africa could be investigated using a molecular approach of the modern remaining taxa.

SUMMARY OF OLD WORLD PODOCARP DISPERSALS AND EXTINCTIONS

PODOCARPUS SENSU LATO

Originating in Gondwana by the earliest Cretaceous, *Podocarpus* was present in India and Africa during the Early Cretaceous but became extinct in West Africa following the mid-Cretaceous denudation of uplands (which may not have occurred in East or South Africa) and became reduced in extent in India following its Late Cretaceous northward drift (Morley, 2000: fig. 8.1). It extended its range to the Ninety East Ridge by the Paleocene and

was present at the same time in Patagonia. Subsequently, *Podocarpus* dispersed presumably from India to the Sunda region during the late Eocene (and possibly at later times from Australia by long-distance dispersal) following global cooling, from which it radiated to its present distribution across the Southeast Asian region. It subsequently expanded to East Asia and may also have extended around the Pacific rim to Alaska at the time of the Miocene climatic optimum. In Africa, it dispersed from East Africa to the West African highlands following further global cooling 2.7 MYA, during the time of expansion of the Northern Hemisphere ice sheets (Figure 2.12).

DACRYDIUM

Dacrydium originated in Australasia (Figure 2.13) during the Late Cretaceous (Santonian, 86 MYA) and dispersed to the Ninety East Ridge by the Paleocene (55 MYA). It then appeared in India 50 MYA during the early Eocene and in East Java at the basal Oligocene (33 MYA). It attained a widespread distribution in Southeast Asia and reached China and Vietnam by the late Oligocene (25 MYA) and Japan during the Miocene thermal maximum (16 MYA). There are also records from the mid-Tertiary of Patagonia.

DACRYCARPUS

Dacrycarpus originated in Australasia during the Maastrichtian (Late Cretaceous, 75 MYA) and was present in Patagonia during the early Eocene. It dispersed to New Guinea during the late Miocene. It established itself in Borneo and Java during the early Pliocene but subsequently dispersed to Sumatra, the Malay Peninsula, and Myanmar during the early Pleistocene.

PHYLLOCLADUS

Phyllocladus producing the typical bisaccate pollen with diminutive sacchi first appeared at the same time in Australia and Patagonia during the Paleocene (Martin, 1994; Wilf et al., 2003). It dispersed to New Guinea in the late Miocene and to Borneo during the earliest Pleistocene.

MICROCACHRYS

Microcachrys was widespread across Australasia and the Indian subcontinent during the Jurassic and Early Cretaceous but disappeared from lower-latitude areas, including India and the New Guinea region, after the Albian (96

MYA). Its latest "low-latitude" location was on the Ninety East Ridge during the Paleocene and Oligocene (Kemp and Harris, 1975).

CONCLUSIONS

The family Podocarpaceae first appeared in the Triassic of Gondwana and apparently spread to the Northern Hemisphere during the Jurassic. However, from the Early Cretaceous onward the family has had an essentially Gondwanan, or Gondwana-derived, distribution. Low-latitude Cretaceous wood fossils, always tentatively attributed to the Podocarpaceae, are thought unlikely to be podocarps since they are not accompanied by bi- or trisaccate pollen, which is ubiquitous in extant podocarps with the exception of the isolated genus *Saxegothaea*. The main podocarp genera diversified in Gondwana during the Cretaceous and earliest Tertiary, coinciding with the opening of the Southern Ocean, and by the Paleocene all the taxa that can be differentiated using pollen were in place. The Podocarpaceae is, with minor exceptions, essentially adapted to areas of wet, equable, mesothermal to microthermal climate, and this has been the case throughout its history. The availability of areas of wet climate and equable mesothermal temperatures has probably impacted on its pattern of dispersal or extinction during the Cenozoic.

At the beginning of the Tertiary, the Podocarpaceae was an important element of the vegetation of Australasia, Antarctica, and southernmost South America, disappearing from Antarctica following mid-Tertiary glaciations.

Podocarpus s.l. may have been present at low latitudes in elevated areas of Africa during the Early Cretaceous and, together with *Microcachrys*, was an important member of the Indian and New Guinea floras (both of which lay south of the tropical zone at that time). Podocarps became of limited distribution on the Indian Plate during the Late Cretaceous following competition from African immigrant angiosperms (Morley, 2000) and possibly the presence of unfavorable climates as the Indian Plate drifted across the Southern Hemisphere high-pressure zone. Aridity and marine transgression were probably responsible for its disappearance from the New Guinea region.

In Southeast Asia, *Podocarpus* s.l. first appeared in the late Eocene in Java, presumably as a result of dispersal from India but also possibly long-distance dispersal from Australia. This was closely followed during the early Oligocene by *Dacrydium*, which probably dispersed into Southeast Asia by island hopping along the Ninety East Ridge and via India (where it subsequently became extinct).

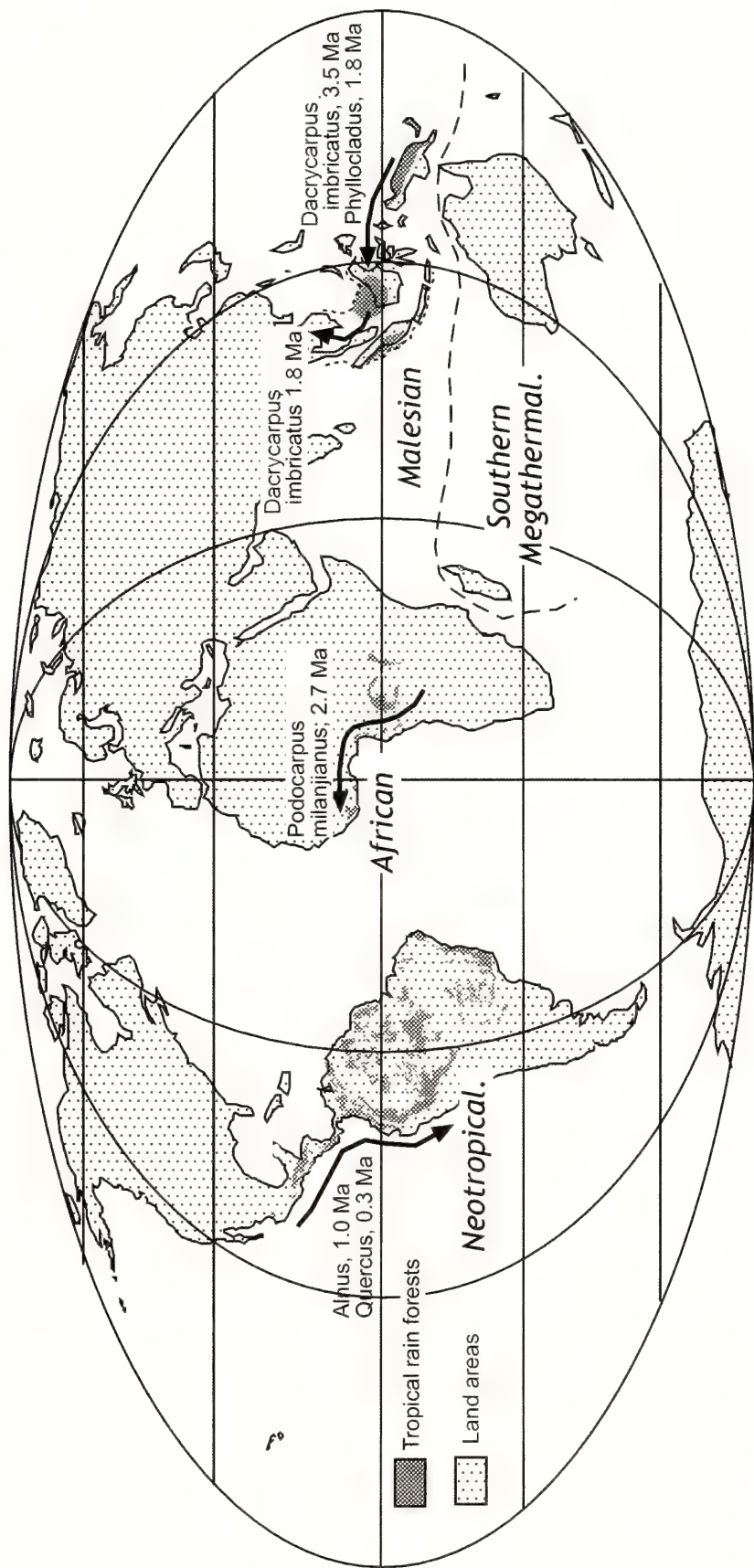


FIGURE 2.12. Dispersal of temperate taxa into low latitudes associated with Quaternary global cooling (from Morley, 2000).

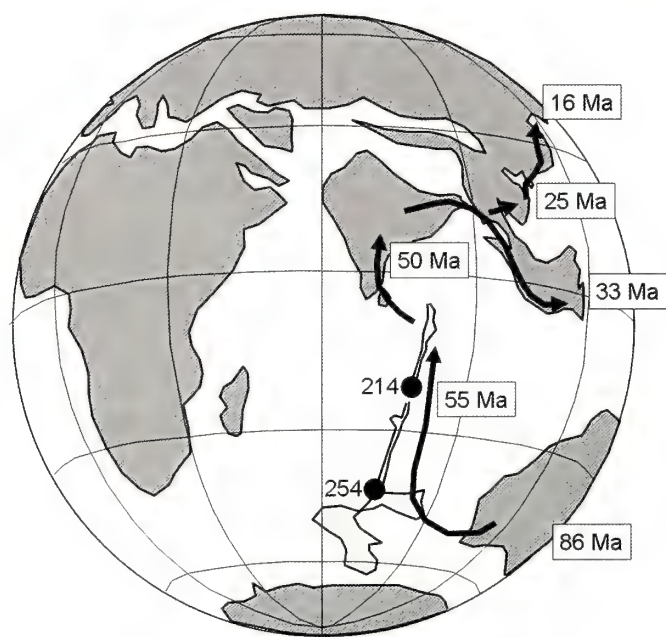


FIGURE 2.13. Dispersal of *Dacrydium* into Southeast and East Asia.

The first members of *Dacrydium* to reach the Sunda region were probably trees of lowland forests and dispersed via nutrient-poor heath forests (kerangas) and peat swamps. Subsequently, some *Dacrydium* species may have found niches in montane forests. *Podocarpus* s.l. was probably a tree of montane forests at the time of initial dispersal, but its widespread occurrence in low-altitude nutrient-poor habitats probably reflects multiple long-distance dispersal events rather than descent from montane species.

Dacrycarpus dispersed from Australia to the mountains of New Guinea as the island formed during the late Miocene. It spread by island hopping into Borneo and Java during the mid-Pliocene and then to the Sumatra and the Malay Peninsula at the beginning of the Pleistocene. It is probably still in the process of range expansion. *Phyllocladus* followed the same route as *Dacrycarpus* to New Guinea during the late Miocene and island hopped to Borneo at the beginning of the Pleistocene.

It is likely that *Podocarpus* s.l. was present in upland areas of the African continent during the mid-Tertiary, enabling dispersal into West Africa by island hopping between areas of montane forest during the mid-Pliocene, coinciding with the time of global climate cooling and the expansion the Northern Hemisphere ice caps.

Although not part of this review, it is intriguing that only *Podocarpus* s.l. dispersed to the neotropics, despite the full diversity of podocarp genera being present in

Patagonia during the early Tertiary and the presence of an appropriate dispersal path in the form of the Andes. It is suggested that unfavorable climates within the Southern Hemisphere high-pressure zone may have inhibited such dispersals.

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Ecology and Distribution of Neotropical Podocarpaceae

James W. Dalling, Phoebe Barkan, Peter J. Bellingham, John R. Healey, and Edmund V. J. Tanner

ABSTRACT. Podocarps are a frequent, but rarely a dominant, component of neotropical wet forests extending from South America into central Mexico and the Greater Antilles. Although podocarps are often considered to be predominantly montane taxa, several species occur in lowland forest and are locally abundant on some Pacific and Atlantic coastal islands in Central America. Here we review literature on the origins and distribution of neotropical podocarps and highlight their apparent association with resource-poor environments. As a consequence of forest conversion and logging, many podocarps that were already habitat specialists are now further restricted to small and increasingly fragmented populations. Unfortunately, there is little information on the regeneration ecology of podocarps with which to assess the recruitment potential of these populations. An exception is the long-term studies of the dynamics of *Podocarpus urbanii*, a common species in montane forest in Jamaica. *Podocarpus urbanii* is moderately shade tolerant and successfully regenerates beneath undisturbed forest. The low juvenile mortality rate of *P. urbanii*, coupled with relatively high diameter growth, suggests that this species and possibly other podocarps may have greater utility for reforestation than is currently recognized.

DIVERSITY OF NEOTROPICAL PODOCARPACEAE

Central and South America harbor a large fraction of global podocarp diversity and are represented by five genera: *Podocarpus* (31 species), *Prumnopitys* (5 species), *Retrophyllum* (2 species), *Saxegothea* (1 species), and *Lepidothamnus* (1 species). Most of these podocarps (excluding the last two genera) have a tropical distribution; the 29 neotropical *Podocarpus* species account for nearly a third of the species currently recognized in the genus (Farjon, 2001). Malaysian podocarps show a diversity of forms, including parasitic, lianescent, and aquatic species on New Caledonia (Enright and Jaffré, this volume), whereas

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neotropical taxa are all canopy trees of mature forest, although a few elfin forest species found on infertile soils (*P. tepuiensis*, *P. sprucei*, *P. buchholzi*) seldom grow more than a few meters tall.

PALEOHISTORY OF NEOTROPICAL PODOCARPACEAE

Podocarpaceae is a monophyletic group of Gondwanan origin with a fossil record dating back to the Early Cretaceous (Krassilov, 1974). Neotropical fossil evidence indicates the presence of podocarps in northern South America at least since the late Eocene to Oligocene (van der Hammen and Hooghiemstra, 2000). The modern distribution of podocarps, however, has been most affected by more recent events. The rise of the Andes from the south to north and west to east first created montane habitats 15 MYA, culminating in the rapid uplift of the Eastern Cordillera during the Pliocene 2–5 MYA (Gregory-Wodzicki, 2000; Antonelli et al., 2009; Graham, 2009). Although little is known about the flora and environment of tropical South America during the Pliocene, sediment records indicate that the principal species in northern Andes forests were the montane taxa *Weinmannia* (Cunoniaceae) and *Podocarpus* (van der Hammen, 1974).

Concurrent with Andean uplift, formation of the Panama land bridge allowed podocarp species to migrate north into Central America and potentially competing species to migrate south into the Andes. Analysis of continuous lake sediments from the plain of Bogota (Eastern Cordillera of the Andes, 2,580 m elevation), spanning the late Pliocene to the Holocene, indicate that podocarps were among the most important taxa in northern Andean forests during interglacial periods up to 330,000 years ago, before being replaced primarily by *Quercus* (oak) forests (van't Veer and Hooghiemstra, 2000). *Quercus* was one of the last immigrants to northern South America a million years ago (van der Hammen, 1989) and became dominant after the last glacial cycle at elevations of 2,000–3,000 m in the northern Andes and through Central America. *Quercus*, however, only extends as far south as the Colombia–Ecuador border (1°N; Hooghiemstra, 2006), so competitive exclusion by oaks cannot account for the rarity of podocarps in southern Andean forests.

Temperature fluctuations associated with glacial cycles may also have induced elevational shifts in podocarp populations. During the Pleistocene, podocarp pollen appears periodically at multiple low-elevation sites (Behling et al., 1999; Haberle and Maslin, 1999; Ledru et al., 2001;

Niemann and Behling, 2008). The occurrence of podocarps at lowland Amazonian sites has been interpreted as key evidence indicating glacial cooling (e.g., Liu and Colinvaux, 1985; Behling, 1998). Comparisons of the presumed extant elevational distribution of podocarps in Andean forests with paleorecords of podocarp pollen has led to an inferred climate cooling of 4.5°C–7.0°C during the Wisconsin glacial maximum (Liu and Colinvaux, 1985; Haberle and Maslin, 1999).

Although extensive pollen records exist for podocarps, glacial migration patterns of individual taxa cannot be corroborated using these data. Pollen identifications are limited to the generic level (Hooghiemstra et al., 2006), and interpretation of low-density pollen records are further affected by the potential for long-distance transport (e.g., Behling, 2001; but see van der Hammen and Hooghiemstra, 2000). However, palynological data, when combined with genetic analyses, provide a useful additional tool to infer the timing of podocarp migration patterns. Ledru et al. (2007) combined pollen records with molecular analysis of living material to infer relationships among 26 populations of three Brazilian endemic species (*P. sellowii*, *P. lambertii*, and *P. brasiliensis*) that occur in diverse forest types: along rivers in Cerrado, mid-elevational *Araucaria* forest, and Atlantic rainforest in southern and eastern Brazil. Clustering in the molecular data indicated that the three podocarps formed three groups: (1) a rather homogeneous group consisting of *P. lambertii*, a species associated with *Araucaria* forest, suggesting recent population expansion in the last 3,000 years in southern Brazil; (2) a more heterogeneous northern group of *P. sellowii* (that also includes *P. brasiliensis*), associated with riverine forest that expanded earlier (~16,000 years ago); and (3) a montane and coastal group from eastern Brazil including both *P. sellowii* and *lambertii*, which are relicts from a population expansion over a short period during the cool and moist conditions of the last glaciations ~29,000 years ago. Combined genetic and palynological approaches now hold promise for understanding the distribution and timing of migration of northern and western Amazonian podocarps.

CURRENT RANGE DISTRIBUTION OF PODOCARPS

Neotropical podocarps have been collected extensively, with metadata available for >1,900 specimens accessible through the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.net>, accessed 10 October

2009). Broad distributional patterns at the genus level are therefore generally well resolved. At the species level, however, taxon boundaries remain poorly differentiated, with some species based on very few specimens (Farjon, 2001). As a consequence, disjunct populations of some taxa continue to be discovered (Neill, 2008). Below, we describe distribution patterns for neotropical taxa recognized by Farjon (2001) based on plots of locality information for herbarium specimens.

The northern distributional limit of podocarps is delimited by *P. matudae*, with an outlying population in cloud forest in Tamaulipas, Mexico, at 23°N (Figure 3.1a). Two other Central American species with broad distributional patterns also extend into Mexico: *P. guatemalensis* occurs at 300 m elevation at the transition between lowland and mesophilic montane forest in Oaxaca and may also extend into the more-mesic forests in the southern Yucatan Peninsula, whereas *P. oleifolius* occurs in lower montane forest at 1,000 m in Veracruz. Elsewhere in Central America podocarp taxa mostly have broad geographic ranges: *P. oleifolius* occurs through to Panama and the Andes as far as Venezuela and northern Peru, *P. guatemalensis* extends to Colombia, and *P. costaricensis* has a narrower range restricted to central Costa Rica and eastern Panama. Two remaining Central American *Podocarpus* taxa recognized by Farjon (2001) are taxonomically more doubtful. *Podocarpus magnifolius* occurs in Bolivia, Peru, and Venezuela, but several additional collections have been made in eastern and central Panama. *Podocarpus monteverdeensis*, which occurs only in central Costa Rica, has been considered a synonym of *P. oleifolius* (Merello, 2003). A single endemic species of *Prumnopitys*, *P. standleyi*, occurs in Costa Rica in high-elevation oak forests.

Two species, *Podocarpus angustifolius* and *P. aristulatus*, occur in Cuba at 20°N–21°N, whereas *P. aristulatus* and *P. hispaniolensis* occur in Hispaniola and *P. purdieanus* and *P. urbanii* occur in Jamaica at 18°N. In contrast to the island endemics of the Greater Antilles, only a single species, *P. coriaceus*, is recognized to occur across the Lesser Antillean islands of Dominica, Guadeloupe, Martinique, Montserrat, and St. Kitts and Nevis, as well as Puerto Rico. An additional endemic species, *P. trinitensis*, occurs on Trinidad.

In South America, most tropical podocarps are distributed along the northern and western Andes or centered on the Guyana Shield of southern Venezuela (Figure 3.1b). Although some taxa have extensive distributions within the Andes (notably *P. parlatorei* in the southern Andes extending north into Bolivia and *P. oleifolius* through Peru, Ecuador, and Colombia), most species are more restricted

in their ranges and exhibit multiple disjunct populations suggestive of habitat specialization or refugial distributions. Three species, *P. magnifolius*, *P. celatus*, and *P. tepuiensis*, maintain populations in both the Guyana Shield and the western Andes. In addition to *Podocarpus*, three species of *Prumnopitys* and one species of *Retrophyllum* are associated with mid-elevation (*P. harmsiana*) and high-elevation (*P. montana*, *P. exigua*, and *R. rospigliosii*) tropical Andean forests.

ELEVATIONAL RANGE DISTRIBUTION OF PODOCARPS

Paleoclimate reconstructions for the neotropics based on podocarp pollen data hinge on the assumption that podocarps are restricted to montane forests. This assumption is clearly violated for Central American taxa, where *Podocarpus guatemalensis*, the most widespread species, has a primarily lowland distribution (Figure 3.2a). *Podocarpus guatemalensis* illustrates that under current climate conditions podocarps are capable of persisting at sea level; GBIF herbarium collection data indicate that *P. guatemalensis* occurs in Caribbean coastal habitat from Belize to Panama and along the Pacific coast from Costa Rica south to Isla Gorgona and the Chocó of Colombia. Elsewhere in South America, *P. guatemalensis* occurs primarily at <1,000 m elevation, with a few collections at 2,600 m in Zamora-Chinchipe, southern Ecuador, representing distributional outliers for this species. No occurrences of this species have been reported east of the Andes.

South American podocarp taxa do have a primarily montane or lower montane distribution, with a few exceptions (Figure 3.2b). Most notably, *P. celatus* occurs in lower montane and lowland forest across the western Amazon of Ecuador and Peru and the northern Amazon of Venezuela. The lowest elevation occurrence of this taxon is at 130 m in Loreto, Peru, where it occurs on infertile lateritic and white sand soils.

In the Greater Antilles, *Podocarpus urbanii* extends to the highest point of Jamaica (2,256 m; Asprey and Robbins, 1953), whereas on Hispaniola *P. aristulatus* scarcely occurs above 1,800 m in the Cordillera Central. *Podocarpus aristulatus* is restricted to cloud forests (1,550–1,800 m), where it is the third commonest tree; above 1,800 m forests are dominated by *Pinus occidentalis* (Martin et al., 2007). The absence of *Podocarpus aristulatus* at higher elevations may be related to fire. Above 1,800 m fires are associated with El Niño droughts, occurring, on average, every seven years (Martin and Fahey,

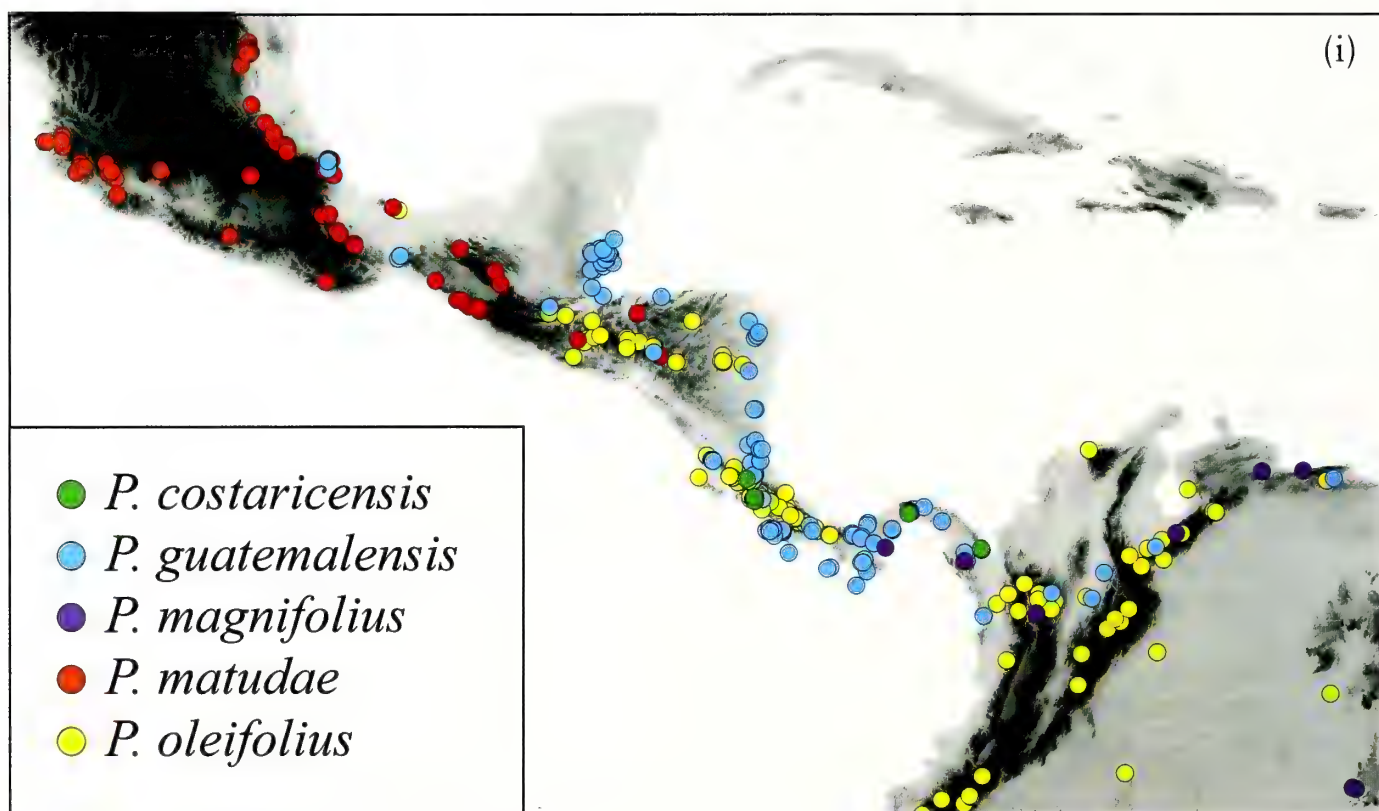
2006). In contrast, lower-elevation cloud forests do not support fire (Martin et al., 2007). On Hispaniola, a constraint on the distribution of *P. aristulatus* imposed by fire is consistent with the great majority of podocarps being intolerant of fire (Coomes and Bellingham, this volume).

HABITAT ASSOCIATIONS OF NEOTROPICAL PODCARPS

The global distribution of conifers suggests a competitive advantage over angiosperms at high latitude and in arid or nutrient-poor environments (Ellenberg, 1988). In tropical and mesic temperate forests, Bond (1989) suggested that conifers have been excluded by their relatively low seedling growth rates, compared with angiosperm competitors. Low-productivity environments may eliminate this competitive disadvantage; inherently slow growth and tissue turnover rates can result in greater use efficiency of nutrients for conifers than angiosperms (Grime, 1979). Recently, Coomes et al. (2005) highlighted an additional mechanism that might account for temperate-forest podocarp distributions. On the South Island of New Zealand,

fertile alluvial terraces are dominated by angiosperms, whereas nearby older, phosphorus-impooverished terraces are dominated by podocarps. However, rather than nutrient availability, Coomes et al. (2005) argued that a dense understory fern layer leading to a thick, slowly decomposing litter layer effectively prevents seedling recruitment of podocarps, whereas smaller-seeded angiosperms are able to establish on less-shaded elevated recruitment sites formed by fallen logs.

Herbarium metadata unfortunately provide little information on the habitat associations of neotropical podocarps, although notes on specimens of *P. celatus*, *P. coriaceus*, *P. ingensis*, and *P. oleifolius* comment on the presence of sandy or quartzite soils, whereas the Cuban endemic species *P. angustifolius* occurs on serpentine soils (identified as *P. ekmannii*) or on lateritic soils that are more organic-rich than those dominated by pine (*Pinus cubensis*) forest (Smith, 1954; Borhidi, 1991). Ideally, evidence for habitat associations could be provided by plot-based ecological studies, but podocarps seldom seem to occur in plots. Almost all neotropical permanent plots are in the Amazonian lowlands, where podocarps are scarce. Podocarps have not been reported from any of the >250



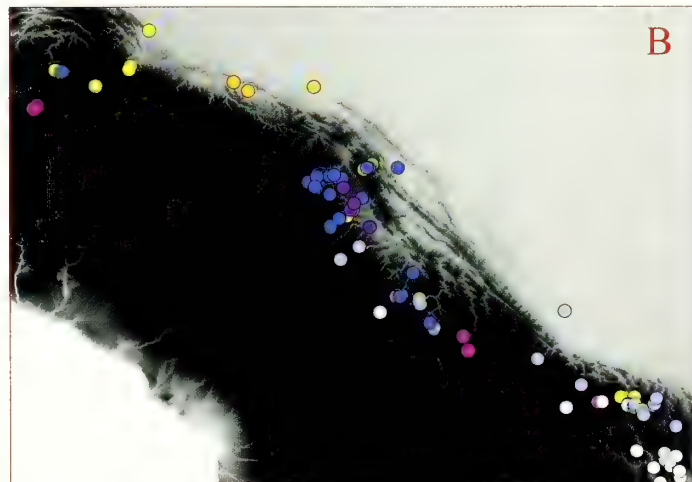
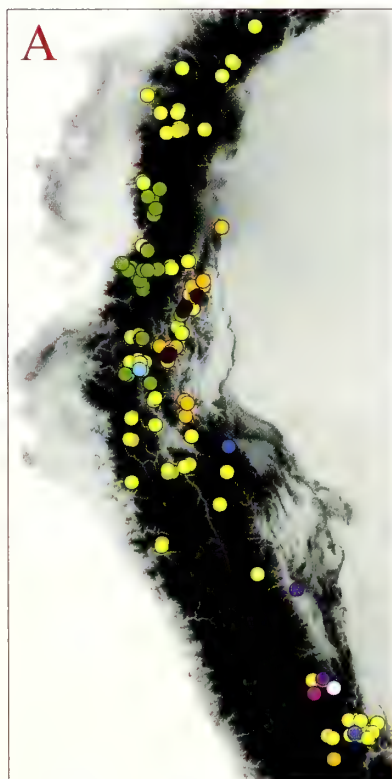
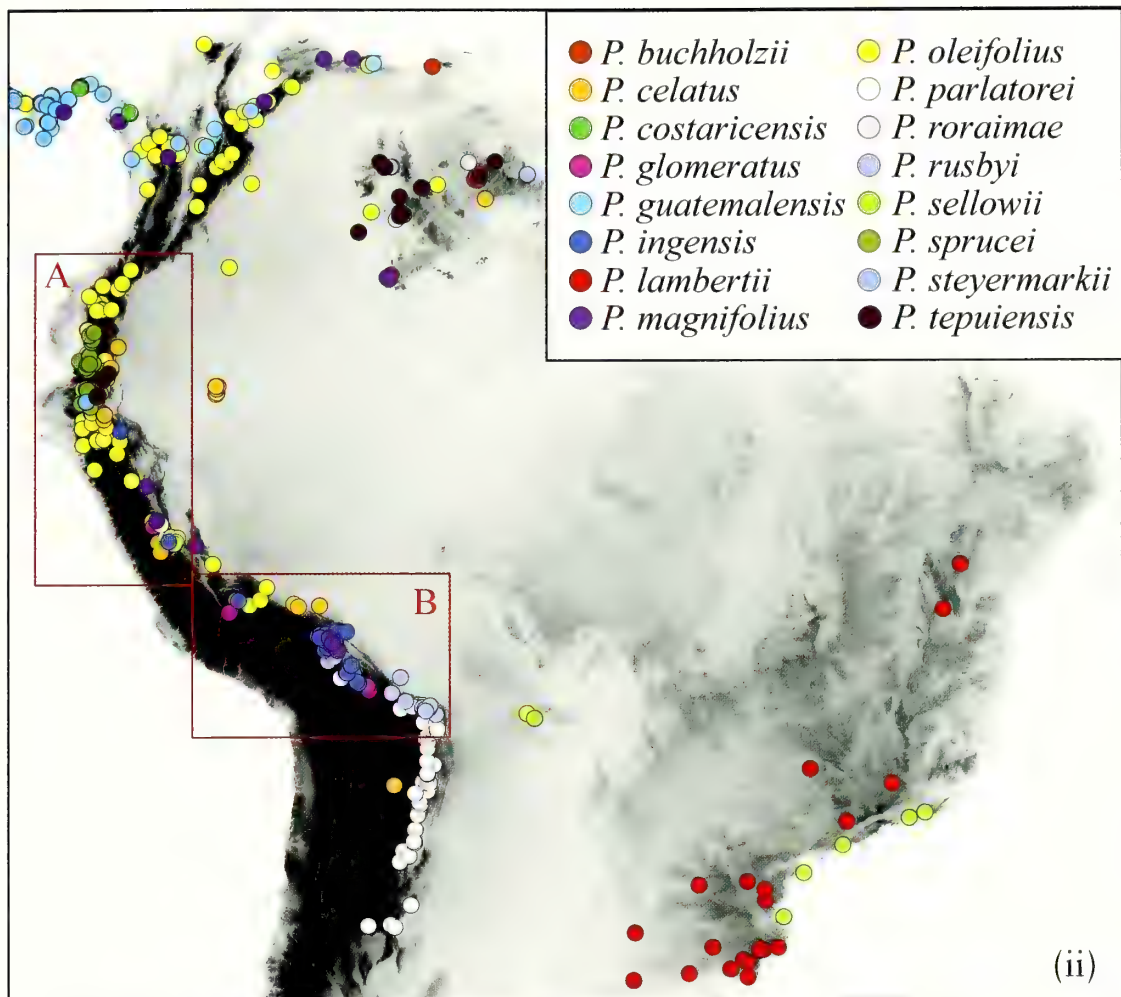


FIGURE 3.1. Collection locations for neotropical *Podocarpus* species in (i, facing page) Central America and (ii) South America based on specimen metadata available through the Global Biodiversity Information Facility (<http://www.gbif.net>). Insets A and B provide enhanced regional detail. Antillean taxa and South American taxa with <10 georeferenced collections are omitted. Collections are plotted on the WorldClim gray-scale elevation surface for the neotropics (Hijmans et al., 2005). Darker shading indicates higher elevations.

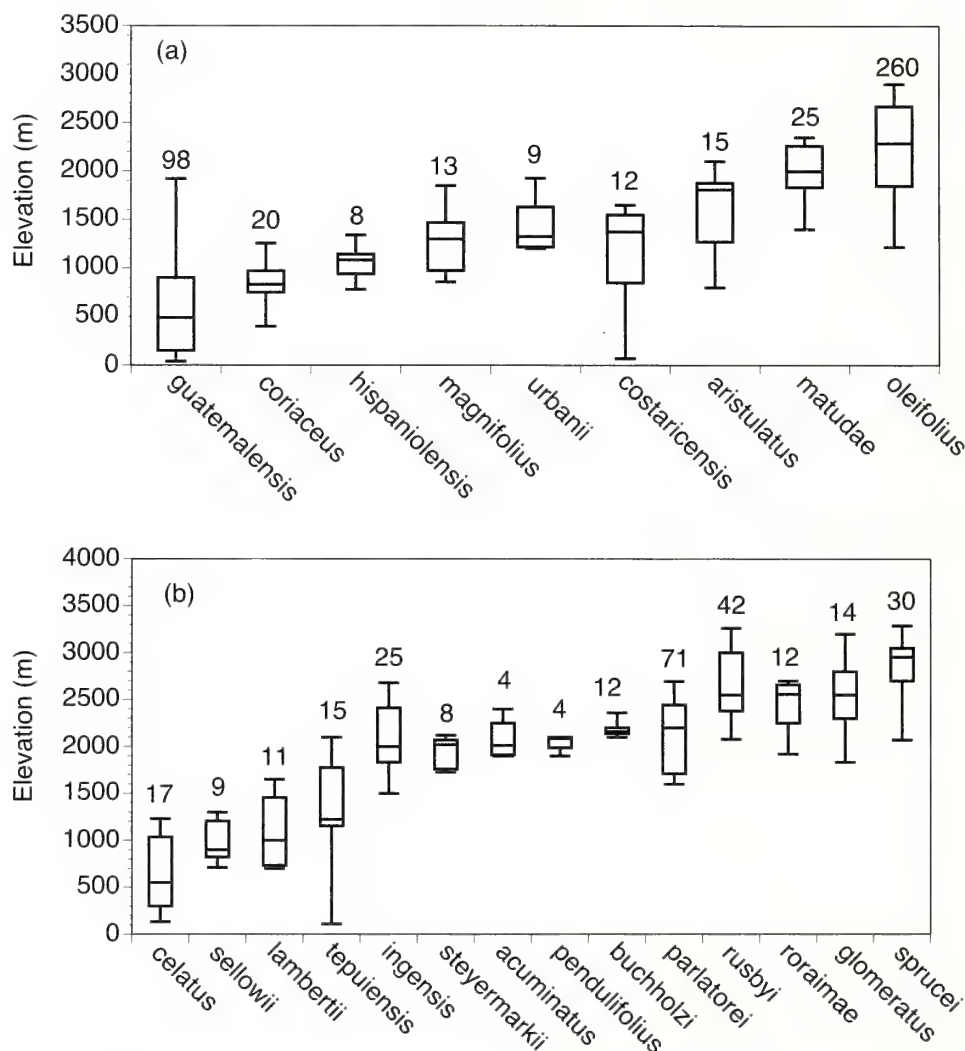


FIGURE 3.2. Box plots showing the median, 10th, 25th, 75th, and 90th percentiles for the elevation ranges of (a) Central American, Antillean, and widespread taxa and (b) South American *Podocarpus* species. Values above each box indicate the sample size for each species. Taxa with less than three elevational records are not included. Species are ordered by median elevation.

ha of the RAINFOR (Amazon Forest Inventory Network) 0.1–1 ha permanent plots arrayed across lowland Amazonia (O. Phillips, University of Leeds, personal communication), nor from lowland and montane 25–50 ha forest plots maintained by the Center for Tropical Forest Science (<http://www.ctfs.si.edu>). Because of their presumably patchy distribution, they are also absent from a network of 1 ha plots in the Colombian Andes (A. Duque, Universidad Nacional de Colombia, personal communication). When present in plots, they tend to occur at low relative density in species-rich forest. For nine *Podocarpus* species recorded in plot inventories, only in four cases did they account for >10% of either basal area or stem density (Table 3.1).

For four *Podocarpus* species, soils data accompanying plot inventories can be used to infer habitat specialization. *Podocarpus oleifolius* is a montane species distributed along the Continental Divide of Central America and the northern Andes. At the Fortuna Reserve in western Panama, *P. oleifolius* has a highly localized distribution: it is restricted to very wet sites with acidic humic soils underlain by a striking white soil developed from rhyolitic tuff (Table 3.1). It is absent from more fertile adjoining andesitic sites with similar elevation and rainfall (Andersen et al., 2010; J. Dalling, unpublished data). *Podocarpus oleifolius* also occurs on highly acidic soils in Venezuela (Kelly et al., 1994) and sandy acidic soils in northern Colombia

TABLE 3.1. Site information, stem density (density, individuals ha⁻¹), and basal area for neotropical permanent forest plots containing *Podocarpus* species. The table is sorted by latitude. See table footnotes for site, census information, and references. A dash (-) indicates that data are not available.

Species	Site	Elevation (m)	Rain (mm)	Soil pH	Basal area		Density		Fisher's alpha
					(m ² ha ⁻¹)	(%)	(ind ha ⁻¹)	(%)	
<i>P. matudae</i>	Mexico ^a	800–1,400	2,500	-	1.1	3.5	83	7.1	-
<i>P. matudae</i>	Mexico ^b	1,800	1,000	-	4.1	5.5	120	5.7	15.1
<i>P. aristulatus</i>	Hispaniola ^c	1,100–2,500	2,000	-	4.2	18.0	32	4.0	8.5
<i>P. hispaniolensis</i>	Haiti ^d	1,280	-	-	14.9	21.0	222	6.3	11.7
<i>P. urbanii</i>	Jamaica ^e	1,580	3,000	4.1	10.1	29.1	420	10.3	10.2
<i>P. urbanii</i>	Jamaica ^f	1,580	3,000	3.6	12.0	26.6	840	15.7	8.5
<i>P. urbanii</i>	Jamaica ^g	1,580	3,000	4.3	8.5	18.0	156	3.9	7.4
<i>P. urbanii</i>	Jamaica ^h	1,580	3,000	3.0	0.7	1.1	117	1.5	3.4
<i>P. urbanii</i>	Jamaica ⁱ	1,760	3,000	3.7	5.5	9.9	225	3.0	-
<i>P. urbanii</i>	Jamaica ^j	1,620	3,000	5.0	2.0	4.6	113	2.5	-
<i>P. urbanii</i>	Jamaica ^k	1,660	3,000	4.1	4.4	6.4	80	1.4	-
<i>Podocarpus</i> spp.	Colombia ^l	2,940	1,500	-	35.9	45.0	120	3.8	12.5
<i>P. oleifolius</i>	Costa Rica ^m	2,300	3,300	-	-	-	20	3.5	11.1
<i>P. oleifolius</i>	Panama ⁿ	1,240	6,200	3.6	0.2	0.4	1	0.1	21.2
<i>P. oleifolius</i>	Panama ^o	1,100	4,300	3.9	2.5	7.8	6	0.6	12.6
<i>P. oleifolius</i>	Venezuela ^p	2,600	2,500	3.5	0.0	0.1	5	0.1	7.3
<i>P. guatemalensis</i>	Panama ^q	200	6,000	5.8	1.4	5.2	12	2.6	10.2
<i>P. sprucei</i>	Ecuador ^r	1,120	-	4.4	0.9	5.2	7	1.2	25.3
<i>P. oleifolius</i>	Ecuador ^r	1,120	-	4.4	0.3	1.9	4	0.7	20.1
<i>P. tepuiensis</i>	Ecuador ^s	1,620	-	4.6	0.9	7.0	9	1.7	21.6
<i>P. selowii</i>	Brazil ^t	10	1,875	-	0.1	0.4	3	0.4	30.3

^a Puig et al. (1987), Gómez Farías, Tamaulipas, 23°3'N, 99°18'W, min dbh = 5 cm; means of nine 0.25 ha plots.

^b Phillips and Miller (2002), Site 49, Sierra de Manantlan, Jalisco, 19°44'N, 104°15'W, min dbh = 2.5 cm; Gentry 0.1 ha transect plot.

^c Martin et al. (2007), Cordillera Central, Dominican Republic, 19°1'N, 70°60'W, min dbh = 10 cm; means of twenty-five 0.05 ha plots.

^d Senterre et al. (2006), Bois Cavalier, Macaya National Park, 18°19'N, 74°9'W, min dbh = 10 cm; 0.063 ha plot.

^e Tanner and Bellingham (2006), wet slope forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, 0.1 ha plot.

^f Tanner and Bellingham (2006), mull ridge forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, 0.1 ha plot.

^g Tanner and Bellingham (2006), col forest ("gap" forest in Tanner, 1977), Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, 0.09 ha plot.

^h Tanner and Bellingham (2006), mor ridge forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, 0.06 ha plot.

ⁱ Bellingham (unpublished), ridge crest forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, mean of six 0.02 ha plots.

^j Bellingham (unpublished), windward slope forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, mean of five 0.02 ha plots.

^k Bellingham (unpublished), leeward slope forest, Blue Mountains National Park, 18°05'N, 76°39'W, min dbh = 3 cm, mean of five 0.02 ha plots.

^l Phillips and Miller (2002), Site 119, Serranía de Perijá, Cesar, 10°30'N, 72°55'W, min dbh = 2.5 cm; Gentry 0.1 ha transect plot, three *Podocarpus* species occur in the plot.

^m Lieberman et al. (1996), Volcan Barva elevational transect, 10°8'N, 84°6'W, min dbh = 10 cm, 1 ha plot.

ⁿ Dalling (unpublished), Quebrada Honda B, Fortuna Forest Reserve, 8°45'N, 82°14'W, min dbh = 10 cm, 1 ha plot.

^o Dalling (unpublished), Quebrada Chorro, Fortuna Forest Reserve, 8°45'N, 82°14'W, min dbh = 10 cm, 1 ha plot.

^p Kelly et al. (1994), Pico Bolívar, Sierra Nevada National Park, 8°35'N, 71°07'W, min dbh = 3.2 cm, 0.22 ha plot.

^q Ibañez (unpublished) La Falla, Coiba Island, 7°30'N, 81°42'W, min dbh = 10 cm, 1 ha plot.

^r Neill (2008), lower Nangarizta plot, Cordillera del Condor, 4°14'S, 78°39'W, min dbh = 10 cm, 1 ha plot.

^s Neill (2008), upper Nangarizta plot, Cordillera del Condor, 4°14'S, 78°39'W, min dbh = 10 cm, 1 ha plot.

^t Negrelle (2002), Volta Velha Reserve, Santa Catarina, 26°4'S, 48°38'W, min dbh = 5 cm, 1 ha plot.

(Marín, 1998) and reaches highest abundance in tannin-rich swamps at Monteverde, Costa Rica (Haber, 2000).

A striking parallel to *P. oleifolius* in Panama is the recent discovery of *P. tepuiensis* growing at 1,600 m along the Ecuador–Peru border (Neill, 2008). *Podocarpus*

tepuiensis was previously thought to be endemic to the Guyana Shield of northwestern South America, where it occurs on sandstone mesas (tepui). In Ecuador, *P. tepuiensis* is restricted to coarse quartzite outcrops dispersed along the Cordillera del Cóndor that consist of mid-Cretaceous

Hollin Formation sandstones. The Hollin Formation is similar to the Guyana Shield mesa sandstones >1,500 km away from which they are ultimately derived. Paired plots established on the Hollin Formation and adjacent granitic substrates showed that podocarps were restricted to sites underlain by sandstone (Neill, 2008).

Another widely distributed species, *P. guatemalensis*, occurs near sea level from Belize to Isla Gorgona on the Pacific coast of Colombia. In Panama, *P. guatemalensis* occurs on numerous Pacific and Atlantic coastal islands, including Coiba, Bastimentos, and Escudo de Veraguas, and occasionally in wet lowland forest on the mainland. On Coiba, *P. guatemalensis* occurs in one of seven 1 ha forest plots (A. Ibañez, Smithsonian Tropical Research Institute, unpublished data). The distribution of *P. guatemalensis* on Coiba appears to be constrained to mafic substrates on the southern side of a geological fault line (A. Ibañez, unpublished data). Although available evidence therefore suggests that podocarps are associated with acidic, infertile soils, this is not always the case. The Caribbean island species *P. aristulatus* and *P. purdieanus* occur in wet forest on karst limestone in central and western Cuba and western Jamaica, respectively (Borhidi, 1991; Bachman et al., 2007), where exposed rock outcrops and steep topography can result in a relatively open forest canopy.

HABITAT ASSOCIATIONS, FUNCTIONAL TRAITS, AND DEMOGRAPHY OF *PODOCARPUS URBANII* IN JAMAICAN MONTANE FOREST

Among the neotropical montane podocarps, our best understanding of relationships of distribution and abundance in relation to geology and soils is for *Podocarpus urbanii*, which is endemic to the Blue Mountains of eastern Jamaica, between 1,370 and 2,256 m (Buchholz and Gray, 1948). The Blue Mountains are composed of granodiorite, mudstones, sandstones, and conglomerates (Grubb and Tanner, 1976), and *P. urbanii* occurs on all of these rock types, although not on local outcrops of limestone (P. J. Bellingham, unpublished data). On the basis of stem density, *P. urbanii* is the fourth most abundant tree species in the upper slope and ridgetop forests of the Blue Mountains, accounting for 7% of stems >3 cm diameter at breast height (dbh) (Tanner and Bellingham, 2006), and the fourth highest basal area, behind three ericoid tree species (*Cyrilla racemiflora*, *Vaccinium meridionale*, and *Clethra occidentalis*; Bellingham et al., 2005).

Podocarpus urbanii occurs across a range of soil types in the Blue Mountains. For example, it occurs in four forest types within 300 m of each other at 1,580–1,600 m that range considerably in soil pH and concentrations of carbon, nitrogen, and phosphorus (Tanner, 1977; Table 3.2). Forest stature declines from a canopy height of 18 to 7 m as soil pH decreases and soil C:N and N:P ratios increase across the sites (Table 3.2), and forest composition varies considerably (Tanner, 1977). *Podocarpus urbanii* is present in all forest types, with the highest proportion of total basal area and stem density occurring in slope forest and mull ridge forests (ridgetop forest lacking a deep litter layer), which have intermediate fertility (Table 3.2). *Podocarpus urbanii* is markedly less abundant in the short-stature mor ridge forest (which has highly acidic soils with high soil C:N and N:P; Table 3.2). The rarity of *P. urbanii* on the mor site is most likely a consequence of the high organic matter content of the mor soils (>47% carbon up to 30 cm soil depth; Tanner, 1977). Mor soils, in turn, derive from nutrient-poor recalcitrant litter produced by trees in the Ericales that dominate the site. A competitive advantage for the Ericales may arise from symbiotic association with ericoid mycorrhizas, which scavenge effectively for organic sources of nitrogen and phosphorus (Read et al., 2004). In the nearby mull ridge forest, bioassay experiments (Tanner, 1977; Healey, 1989), a field fertilization experiment (Tanner et al., 1990), and a root ingrowth experiment (Stewart, 2000) all indicate colimitation to plant growth by both nitrogen and phosphorus.

A more-extensive view of relationships between *P. urbanii* and site and soil variables is derived from 15 permanent plots within a 250 ha portion of the western part of the Blue Mountains centered on the axial range (plots 1,470–1,900 m, Bellingham et al., 2005; one plot at 1,300 m is below the lower altitudinal limit of *P. urbanii*). *Podocarpus urbanii* occurred in 12 of these plots, within which it comprised 1%–10% of stems ≥ 3 cm dbh (2004 census) and 1%–22% of stand basal area. The percentage of stems and basal area in the plots composed of *P. urbanii* was unrelated to altitude and slope ($r^2 < 0.18$, $p > 0.12$). The percentage of stems and basal area had a unimodal response to soil pH (most frequent in plots with soil pH 3.5–4.2 and not found in plots with soil pH > 5.0; range across plots: 3.1–5.7). The percentage of stems was positively related to soil C:N ratio ($r^2 = 0.30$, $p = 0.03$), but the percentage of basal area was not ($r^2 = 0.16$, $p = 0.14$), and both were unrelated to soil N:P ratio or total phosphorus concentration ($r^2 < 0.09$, $p > 0.28$).

In the Jamaican montane forests, *P. urbanii* has a specific leaf area 55 cm² g⁻¹, which is 32% less than the

TABLE 3.2. Percentage of total basal area and total stem density of *Podocarpus urbanii* (stems ≥ 3 cm diameter at 1.3 m) in four montane rainforest types within 300 m of each other in the Blue Mountains, Jamaica (1580–1600 m elevation; 2004 census), and canopy height and soil characteristics of each forest type. Data are from Grubb and Tanner (1976), Tanner (1977), and Tanner and Bellingham (2006).

Characteristic	Col	Slope	Mull	Mor
Total basal area ($\text{m}^2 \text{ha}^{-1}$)	58 ± 5.2	57 ± 3.7	45 ± 2.7	62 ± 6.7
<i>P. urbanii</i> basal area (%)	17 ± 5.3	22 ± 2.3	23 ± 3.1	2 ± 1.3
Total stem density (stems ha^{-1})	4320 ± 277	4490 ± 318	6220 ± 313	8180 ± 512
<i>P. urbanii</i> stem density (%)	4 ± 1	13 ± 1.1	9 ± 1	2 ± 1
Canopy height (m)	12–18	8–13	8–13	(4–)5–7
Soil pH	4.3	4.1	3.6	3.0
Soil total carbon (%)	11.0 ± 1.4	9.1 ± 1.5	11.6 ± 1.5	49.0 ± 1.2
Soil total nitrogen (%)	1.1 ± 0.12	0.68 ± 0.08	0.88 ± 0.10	2.0 ± 0.03
Soil total phosphorus (%)	0.07 ± 0.01	0.04 ± 0.01	0.04 ± 0.01	0.05 ± 0.00
Soil C:N ratio	10 ± 0.3	13 ± 0.8	13 ± 0.4	24 ± 0.9
Soil N:P ratio	15.7 ± 1.3	20.4 ± 8.7	23.7 ± 5.5	43.8 ± 3.5
Foliar nitrogen (%), all species (<i>n</i>)	1.76 (8)	1.27 (9)	1.61 (14)	1.05 (13)
Foliar nitrogen (%), <i>P. urbanii</i>	0.86	0.71	0.71	0.69
Foliar phosphorus (%), all species (<i>n</i>)	0.10 (8)	0.08 (9)	0.07 (14)	0.05 (13)
Foliar phosphorus (%), <i>P. urbanii</i>	0.05	0.05	0.05	0.05

average ($81 \text{ cm}^2 \text{g}^{-1}$) across 26 species in the forests, and a leaf thickness of $527 \text{ }\mu\text{m}$, which is more than double the average ($237 \text{ }\mu\text{m}$) across 50 species in these forests (Tanner and Kapos, 1982). Across the four adjacent forest types described by Tanner (1977), the foliar nitrogen concentration of *P. urbanii* was consistently less than the average across co-occurring angiosperm species in each site (Table 3.2), whereas the foliar phosphorus concentration of *P. urbanii* was less than average in all but the very nutrient-poor mor ridge forest (Table 3.2). The lower foliar nitrogen concentration in a Jamaican montane podocarp compared to coexisting angiosperms is consistent with results from a temperate rainforest soil chronosequence (Richardson et al., 2005), although in that chronosequence foliar phosphorus concentrations of podocarps were generally not different from co-occurring angiosperms, in contrast to Jamaica.

The montane forests in which *P. urbanii* occurs are subject to frequent but irregular disturbance by hurricanes (with severe canopy damage, on average, every 25 years) and, locally, by landslides triggered by high-intensity rainfall and earthquakes. Comparative data for *P. urbanii* and coexisting angiosperms include a 30-year record of growth and survivorship in permanent plots (Tanner and Bellingham, 2006), seedling recruitment in experimental

tree fall gaps and undisturbed forest (Healey, 1990) and on a chronosequence of landslides (Dalling, 1994), and surveys of tree recovery from hurricane damage (Bellingham et al., 1994, 1995; Bellingham and Tanner, 2000).

Pooling data from across four forests of contrasting soils and forest composition (Tanner, 1977), the tree size structure of *Podocarpus urbanii* shows a distribution skewed toward smaller sizes, with more small stems than two coexisting angiosperm canopy dominants, *Clethra occidentalis* and *Lyonia octandra*, but fewer small stems than *Hedyosmum arborescens* (Bellingham et al., 1995). The size structure of *P. urbanii* is similar to some podocarps in other tropical montane rainforests (e.g., *Falcatifolium falciforme*, Aiba et al., 2004) and warm temperate rainforests (e.g., *Nageia nagi*, Kohyama, 1986) and suggests that *P. urbanii* is at least moderately shade tolerant, which is consistent with its relatively high abundance as seedlings under intact canopies (Figure 3.3; Sugden et al., 1985; Healey, 1990). However, its size structure has not been constant in these permanent plots over 30 years. In 1974, at least 23 years after the forest had last been disturbed by a hurricane, small stems ($<10 \text{ cm dbh}$) were common, and there were few large stems ($>25 \text{ cm dbh}$; Figure 3.4). Hurricane Gilbert, the most powerful North Atlantic hurricane in the twentieth century, severely disturbed these

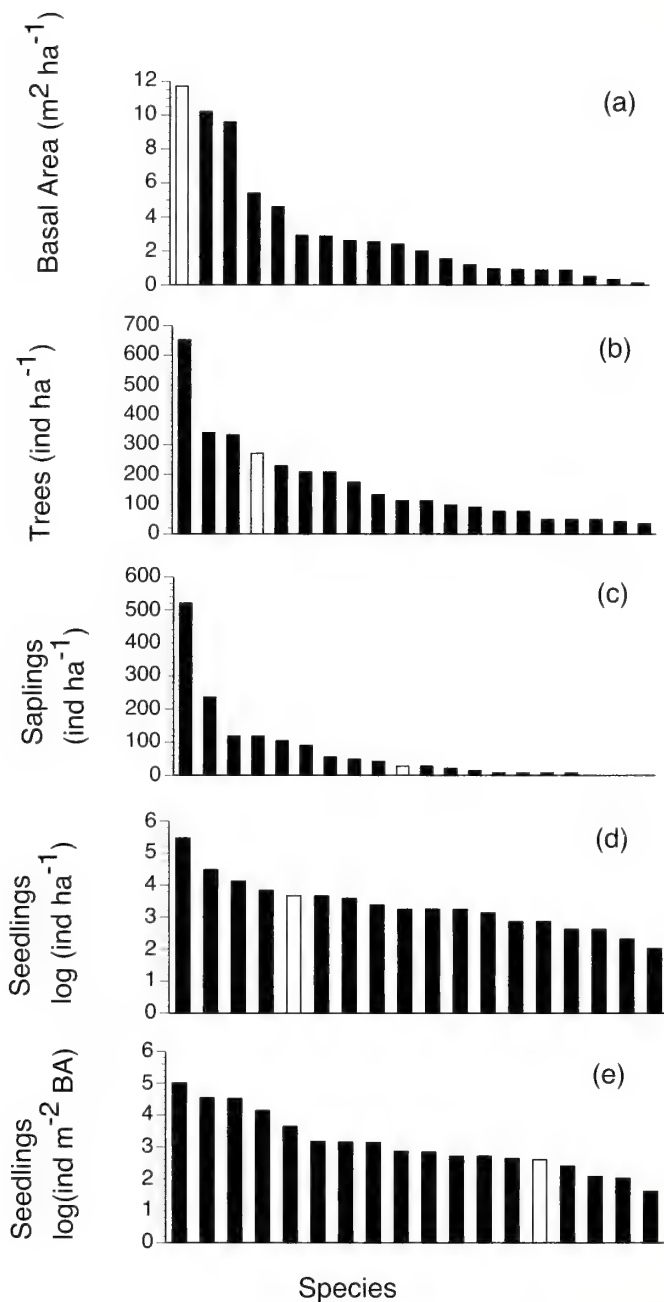


FIGURE 3.3. (a) Basal area, (b) stem density (individuals <3.2 cm diameter at 1.3 m height), (c) sapling density (individuals <3.2 cm diameter at breast height and >3 m height), (d) seedling density, (e) seedling number per unit basal area for all species (solid bars), and *P. urbanii* (open bars). Adult and sapling data are from six 0.024 ha plots; seedling data are from ninety-six 1 m^2 plots. Data are from Healey (1990).

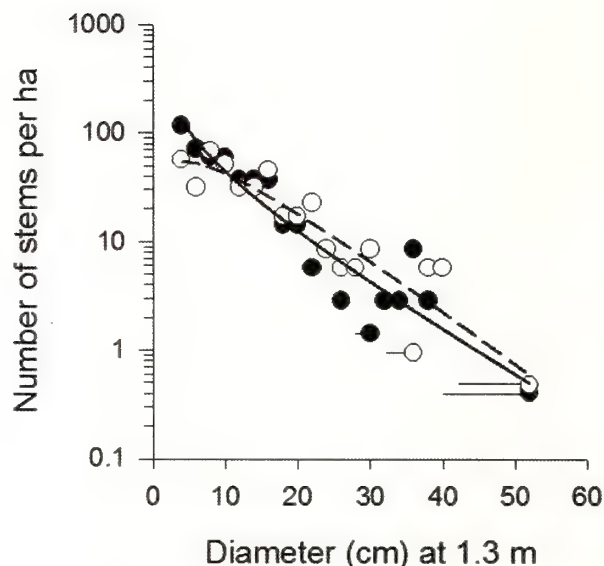


FIGURE 3.4. Frequency distribution of stems of *Podocarpus urbanii* ≥ 3 cm diameter at 1.3 m height, pooled across four forest types within 300 m of each other in the Blue Mountains, Jamaica (total area sampled = 0.35 ha) at two censuses of the same plots (1974, solid circles; and 2004, open circles). Data are in 2 cm interval classes, with averaged interval classes linked by a left-tailed horizontal bar. Curve fitting followed Kohyama (1986) and provided a better fit than the Weibull function (Bailey and Dell, 1973). Solid line (1974): $\ln(y) = 5.075 - 0.08148x - 0.6563\ln(x)$, $r^2 = 0.89$; dashed line (2004): $\ln(y) = 2.684 - 0.1226x + 0.5334\ln(x)$, $r^2 = 0.85$.

forests in 1988 (Bellingham et al., 1995). Sixteen years later, in 2004, there was a greater frequency of stems >20 cm dbh, but many fewer stems <10 cm dbh than in 1974 (Figure 3.4).

Over the past 30 years, mortality rates for *P. urbanii* were between two- and sevenfold lower than co-occurring species on slope, mull ridge, and col forests but similar to co-occurring species on the infertile mor ridge site (Figure 3.5a). Differences in mortality rates among sites probably reflect spatial heterogeneity in tree mortality resulting from Hurricane Gilbert in 1988 linked to ridge and slope topography (Bellingham, 1991). The low mortality of *P. urbanii* relative to co-occurring species does not appear to be a consequence of structural traits. *Podocarpus urbanii* has the fourth lowest wood density in the community (0.6 g cm^{-3} ; Tanner, 1977) and above-average diameter growth rates at all sites except the mor ridge (Figure 3.5b). Recruitment rates into the 3 cm dbh class, however, have been exceptionally low at all sites (Figure 3.5c), and there is little contribution of resprouting to population

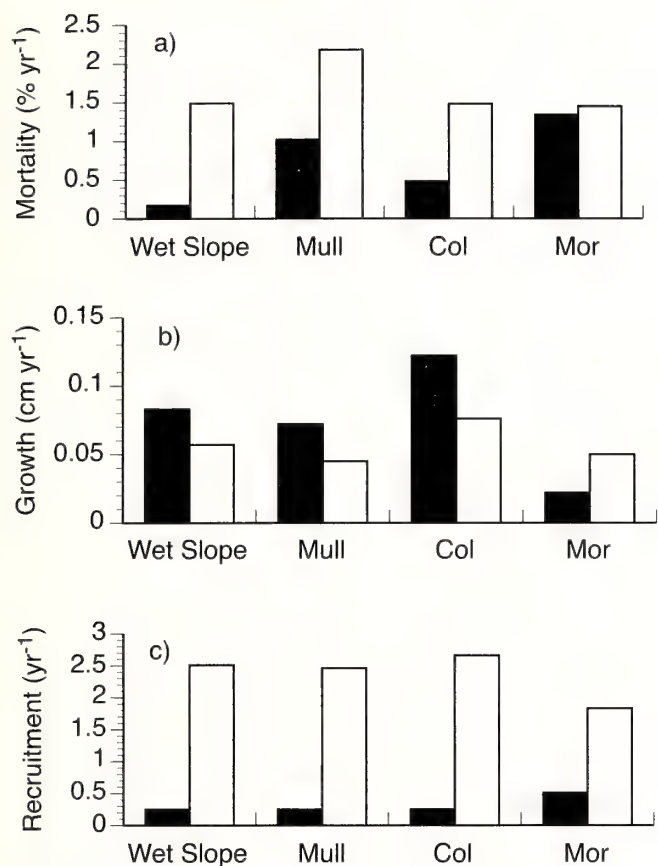


FIGURE 3.5. Annualized (a) mortality, (b) growth, and (c) recruitment rates of *Podocarpus urbanii* (solid bars) and all other species (open bars) from 1974 to 2004 for individuals >3 cm dbh at four forest types in the Blue Mountains, Jamaica (see Table 3.2). *Podocarpus*, all sites combined, mortality (calculated from a census of $n = 136$), recruitment ($n = 11$), growth ($n = 136$). Other species, all sites combined, mortality ($n = 1417$), recruitment ($n = 904$), growth ($n = 822$). Mortality and recruitment rate calculations follow Burslem et al. (2000).

maintenance of *P. urbanii*, in contrast to many of the co-existing angiosperms (Bellingham et al., 1994).

Differences in adult growth and mortality rates among species in part reflect differences in susceptibility to hurricane damage. *Podocarpus urbanii* was significantly more resistant to hurricane damage than the community average when assessed up to four years after Hurricane Gilbert (Bellingham et al., 1995), but the decline in recruitment between 1974–1984 and 1994–2004 suggests that its comparative abundance may derive from periods of relatively less disturbance. Evidence to support this view derives from a study of experimental canopy gaps, similar

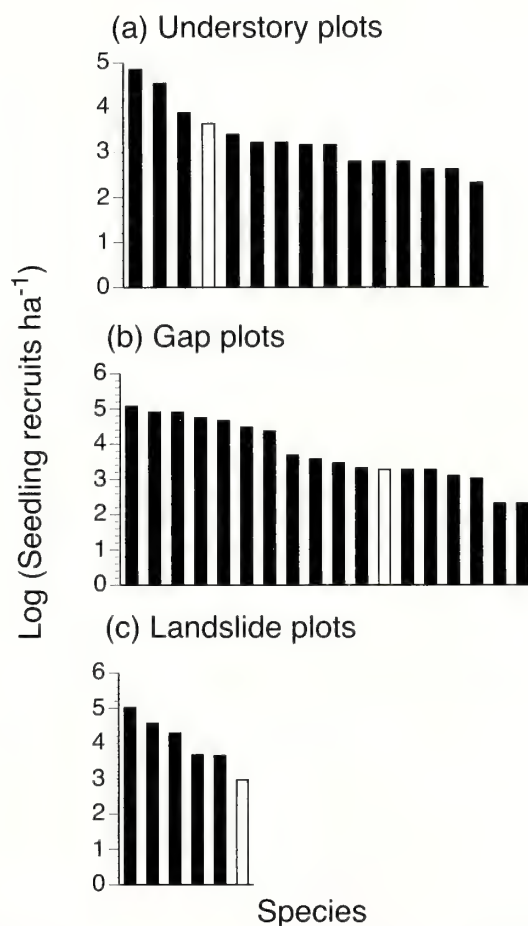


FIGURE 3.6. Density of new seedling recruits per hectare of principal canopy species recorded in forty-eight 1 m² plots distributed across (a) three understory plots and (b) three forest gaps simulating hurricane damage, 18 months after an initial survey. (c) Seedling recruits recorded on four 14-year-old landslides triggered by road construction. Data are from Healey (1990) and Dalling (1992).

to those formed during Hurricane Gilbert, in which *P. urbanii* was the twelfth most abundant species as seedlings compared with being the fourth most abundant species as seedlings under adjacent closed canopies (Healey, 1990; Figure 3.6a,b). *Podocarpus urbanii* may also benefit from other more patchy and less frequent disturbances such as landslides (Dalling, 1994; Figure 3.6c), although observations of recruitment on older (>50 years old) landslides (Dalling, 1994) suggest that they are much more important recruitment sites for ericoid canopy trees.

In summary, *Podocarpus urbanii* is a moderately shade-tolerant tree species in Jamaican montane forest,

capable of regenerating from seed in undisturbed forest more frequently than many of the other principal canopy species. *Podocarpus urbanii* leaf traits and low adult mortality rates are also consistent with shade tolerance. However, *P. urbanii* maintains surprisingly high diameter growth rates, which is probably attributable to its relatively low wood density and may help explain the frequency of this species in hurricane-prone forest.

CONSERVATION AND MANAGEMENT OF NEOTROPICAL PODOCARPS

Of 31 neotropical podocarps, 11 are considered at risk (near-threatened to endangered), 13 are of "least concern," and 5 species lack sufficient data to be evaluated (International Union for Conservation of Nature [IUCN], 2009). Taxa of least concern either have widespread distributions, with populations within protected areas (e.g., *Podocarpus oleifolius*, *P. guatemalensis*), or are restricted to remote, undisturbed rainforests, principally in the Guyana Shield or western Andes. With the exception of *Podocarpus coriaceus*, which occurs on multiple Lesser Antillean islands, all podocarp taxa that occur in the insular Caribbean are of conservation concern. Most threatened are the three Greater Antilles endemics, *P. hispaniolensis*, *P. angustifolius*, and *P. purdieanus*, each of which has restricted distributions on Hispaniola, Cuba, and Jamaica, respectively. Species for which data are insufficient to make a status evaluation include the Trinidad endemic, *P. trinitensis*, and taxa whose distributions are either restricted or scattered or in localities where logging or forest conversion may threaten populations in the future.

In the absence of information on population size or growth, IUCN designation of threatened species must rely heavily on criteria based on observed range size. Our review, indicating that many podocarps are associated with infertile soils, suggests that the large observed geographic ranges (Figure 3.1) of many species may support only small, localized, and therefore unconnected populations. For example, the range distribution of *Prumnopitys harmsiana* includes portions of Venezuela, Colombia, Ecuador, Peru, and Bolivia. However, in Colombia the species is known from only five small populations 600 km apart (Cogollo, 2007). The predominantly mid-elevational distribution of many podocarp taxa (Figure 3.2) has also meant that many populations have been drastically reduced by forest clearance for coffee cultivation, pasture, and row crops (Cogollo, 2007).

In addition to land conversion, several podocarp species have been logged extensively in Colombia and probably elsewhere (Torres-Romero, 1988; Cogollo, 2007). Species that reportedly formed high-density stands, including *Retrophyllum rospigliosii* and *Podocarpus guatemalensis*, are now almost extinct in the Rio Magdalena valley (Torres-Romero, 1988). As yet, few efforts at ex situ conservation of neotropical podocarps have been attempted; however, several species in Antioquia, Colombia, including *R. rospigliosii*, have been promoted for watershed reforestation or have been established in arboreta (Velasquez-Rua, 2005).

Attempts at propagating podocarp seedlings for reforestation have met with limited success. Marín (1998) notes that germination and establishment success of *Podocarpus oleifolius* and *Prumnopitys harmsiana* seedlings are low, whereas propagation of cuttings using plant hormone treatments or removal of established seedlings from wild populations has been more effective. Poor seedling establishment success may also account for the relative paucity of *Podocarpus urbanii* in secondary forest when compared to nearby old-growth forest sites (McDonald and Healey, 2000). Growth and survival trials of seedling transplants, however, indicate that *P. urbanii* performs well above average relative to other Jamaican montane forest trees (McDonald et al., 2003), suggesting that podocarps may have unrealized potential for reforestation.

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Ecology and Distribution of the Malesian Podocarps

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ABSTRACT. Podocarp species and genus richness is higher in the Malesian region than anywhere else on earth, with maximum genus richness in New Guinea and New Caledonia and maximum species richness in New Guinea and Borneo. Members of the Podocarpaceae occur across the whole geographic and altitudinal range occupied by forests and shrublands in the region. There is a strong tendency for podocarp dominance of vegetation to be restricted either to high-altitude sites close to the limit of tree growth or to other sites that might restrict plant growth in terms of water relations and nutrient supply (e.g., skeletal soils on steep slopes and ridges, heath forests, ultramafic parent material). Although some species are widespread in lowland forests, they are generally present at very low density, raising questions concerning their regeneration ecology and competitive ability relative to co-occurring angiosperm tree species. A number of species in the region are narrowly distributed, being restricted to single islands or mountain tops, and are of conservation concern. Our current understanding of the distribution and ecology of Malesian podocarps is reviewed in this chapter, and areas for further research are identified.

INTRODUCTION

The Malesian region has the highest diversity of southern conifers (i.e., Podocarpaceae and Araucariaceae) in the world (Enright and Hill, 1995). It is a large and heterogeneous area, circumscribing tropical and subtropical lowland to montane forest (and some shrubland) assemblages, extending from Tonga in the east to India in the west and from the subtropical forests of eastern Australia in the south to Taiwan and Nepal in the north (Figure 4.1). As a natural entity, the region is best defined by the distribution of closed forests with tropical affinity (Webb and Tracey, 1981; Whitmore, 1984). The Podocarpaceae is the largest conifer family in the region in terms of genera and species, and the genus *Podocarpus* is both the most numerous and widespread (Table 4.1, Appendix).

The taxonomy of the Podocarpaceae in this region has been extensively described by de Laubenfels (1969, 1985, 1987, 1988), who continues to add

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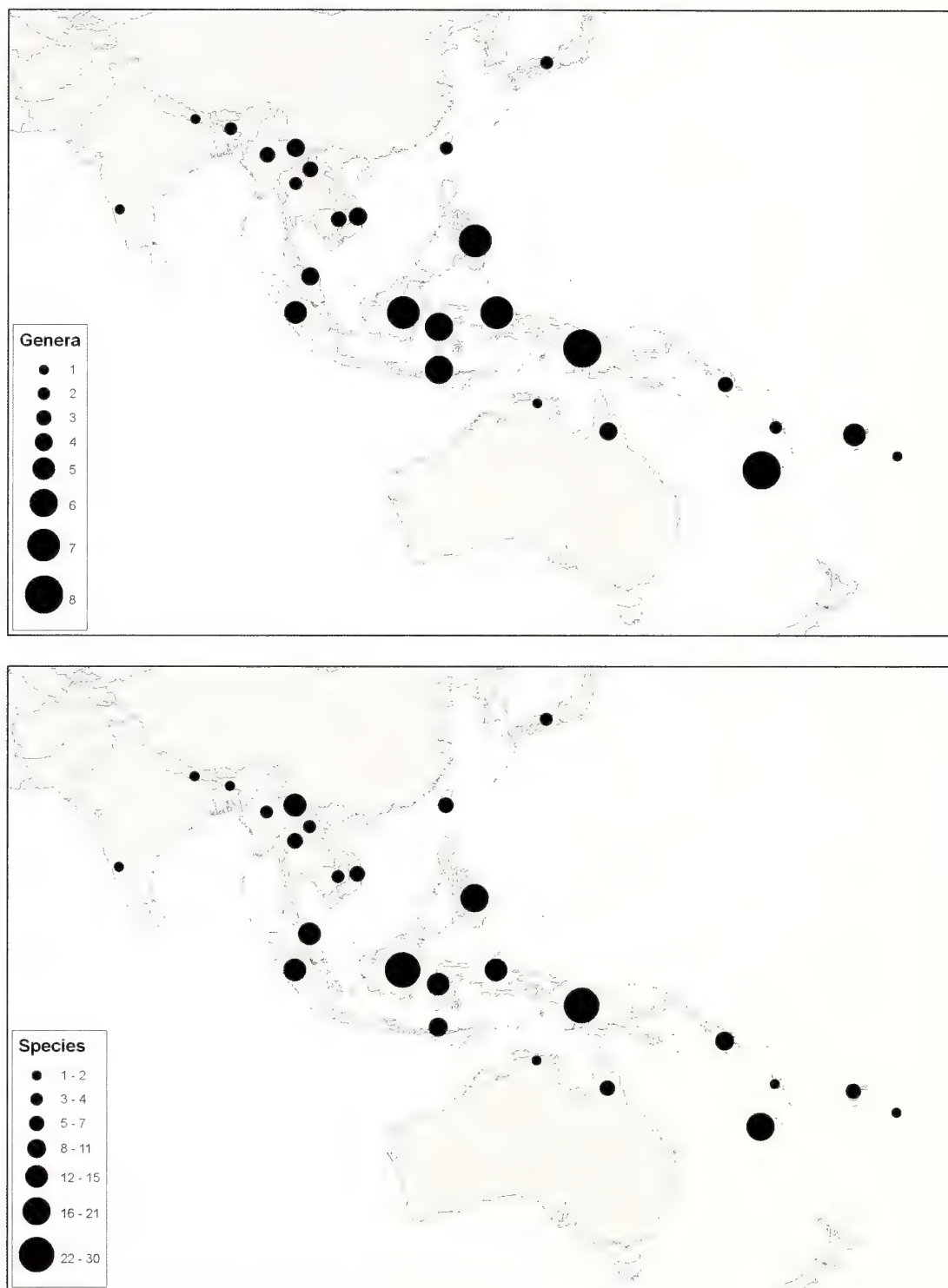


FIGURE 4.1. Malesian distribution of (top) genera and (bottom) species in the family Podocarpaceae, showing nodes of maximum genus diversity in New Caledonia and New Guinea, high levels in eastern Indonesia to the Philippines, and nodes of maximum species diversity in New Guinea and Borneo. Information for southern Australia and New Zealand is not shown. Although outside the region discussed here, data are shown for Japan to indicate the northern range limit for Podocarpaceae globally. (Figure prepared by H. Kobryn.)

TABLE 4.1. Malesian distribution of genera and species in the family Podocarpaceae, showing the total species in each genus and the percentage of the global total occurring within the region. Data were compiled from de Laubenfels (1969, 1985, 1987, 1988, 2003, 2005), Silba (1986, 1987), Enright and Hill (1995), Farjon (1998, 2008), and the Gymnosperm Database (<http://www.conifers.org/index.html>).

Distribution	<i>Acmopyle</i>	<i>Dacrycarpus</i>	<i>Dacrydium</i>	<i>Falcatifolium</i>	<i>Nageia</i>	<i>Parasitaxus</i>	<i>Phyllocladus</i>	<i>Podocarpus</i>	<i>Prumnopitys</i>	<i>Retrophyllum</i>	<i>Sundacarpus</i>	Total
Tonga	0	0	0	0	0	0	0	1	0	0	0	1
Fiji	1	1	2	0	0	0	0	2	0	1	0	7
New Caledonia	1	1	4	1	0	1	0	9	1	2	0	20
Vanuatu	0	1	0	0	0	0	0	1	0	0	0	2
Solomon Islands	0	1	4	0	0	0	0	6	0	0	0	11
NE Australia	0	0	0	0	0	0	0	4	1	0	1	6
New Guinea	0	5	7	1	1	0	1	14	0	1	1	31
Moluccas	0	2	3	0	1	0	1	6	0	1	1	15
Sulawesi	0	3	4	0	1	0	1	5	0	0	1	15
Sunda Islands	0	1	1	1	1	0	0	3	0	0	1	8
Borneo	0	4	7	2	3	0	1	12	0	0	1	30
Sumatra	0	2	4	0	2	0	0	7	0	0	1	16
Malaya	0	1	5	0	2	0	0	6	0	0	0	14
Vietnam	0	1	1	0	2	0	0	3	0	0	0	7
Laos	0	1	1	0	1	0	0	0	0	0	0	3
Thailand	0	0	0	0	2	0	0	3	0	0	0	5
Cambodia	0	0	1	0	1	0	0	1	0	0	0	3
Assam	0	0	0	0	1	0	0	1	0	0	0	2
India	0	0	0	0	1	0	0	0	0	0	0	1
Nepal	0	0	0	0	0	0	0	1	0	0	0	1
China	0	1	1	0	3	0	0	7	0	0	0	12
Philippines	0	2	3	1	1	0	1	11	0	0	1	20
Taiwan	0	0	0	0	1	0	0	5	0	0	0	6
Burma	0	1	0	0	1	0	0	2	0	0	0	4
TOTAL SPECIES	2	8	20	5	6	1	1	55	2	3	1	104
GLOBAL SPECIES	2	9	21	5	6	1	5	106	9	5	1	195
PERCENT MALESIAN	100	89	95	100	100	100	20	52	22	60	100	54

new species to the group (de Laubenfels, 2003, 2005). New Guinea (31 species), Borneo (30 species), and New Caledonia (20 species), followed by the Philippines and Peninsular Malaysia, show the highest levels of species diversity in the region (Figure 4.1, bottom). Tropical eastern Australia is notable for its lower diversity of podocarps (six species, four genera) relative to tropical regions to

the north and east and New Zealand and Tasmania to the temperate south. Even Fiji has higher diversity at the genus level (five genera). Lowest diversity is associated with extreme isolation, with one species each in Tonga in the southeast and India in the west. Low podocarp diversity in the Australian tropics may reflect species losses due to the impacts of Pleistocene climate change associated with

glacial–interglacial cycles and the increased occurrence of fire, which has relegated closed forests to fire-protected moist gullies in many areas (Webb and Tracey, 1981; Kershaw, 1988). In India, low podocarp diversity is likely to be associated with plate tectonic and climate history since the Late Cretaceous, whereas in some tropical islands (e.g., Vanuatu) it is associated with recent geological formation (Enright and Gosden, 1992). Local radiation of species appears to be the major source of species diversity in areas characterized by high numbers of endemic species (e.g., New Caledonia, Borneo), especially within the genus *Podocarpus*.

Conifers are often characterized by great longevity and a low potential rate of population increase relative to angiosperm competitors (Loehle, 1988), which may place them at a competitive disadvantage under either low-stress or high-disturbance regimes (Grime, 1979). Bond (1989), Midgley and Bond (1989), and Midgley (1991) emphasized functional constraints on growth rate in their analyses of the reasons for the decline of conifers relative to angiosperms at the evolutionary timescale. They argued that conifers have a less-efficient vascular system than angiosperm trees since their tracheids are generally more resistant to solute flow than are angiosperm vessels and their leaves are not as fully vascularized. This has limited the range of possible leaf sizes and shapes in conifers and, they argued, helps to explain why conifers are rarely prominent in shaded habitats. Subsequent experimental studies and reviews by Brodribb and colleagues (Brodribb and Hill, 1998, 1999, 2004; Brodribb et al., 2005), Becker (2000), and others (Pammenter et al., 2004; Coomes et al., 2005) support this contention, illustrating that conifers generally have lower hydraulic efficiency and so are disadvantaged under high potential productivity conditions (see Brodribb, this volume). However, under low-light conditions this competitive disadvantage relative to angiosperms declines (but is not eliminated), and under a combination of low-light and low-nutrient conditions, such as in some tropical forests, the disadvantage may disappear altogether (Becker, 2000; Pammenter et al., 2004). Given these constraints, the Podocarpaceae are undoubtedly the most successful of all conifers, with a large number of species showing a broad range of leaf adaptations, facilitating persistence in a range of tropical (and temperate) forests from sea level to altitudinal tree line and beyond.

Population size structures for conifers in both tropical and southern temperate forests are frequently discontinuous, with regeneration gaps evident in the sapling and small tree stages (Clayton-Greene, 1977; Veblen and Stewart, 1982; Veblen and Lorenz, 1987; Stewart and Rose,

1989; Burns, 1991; Lara, 1991; Lusk and Ogden, 1992). Demographic studies have generally shown that such discontinuities in stage structures are typically local in extent and can be explained by differential response to disturbances at local to landscape scale, with the conifers often characterized as long-lived colonizers (e.g., Ogden, 1985; Enright, 1995; Enright et al., 1999). Although this may be true for podocarp species that dominate high-altitude forests in parts of tropical Malesia, the population dynamics of many species present at lower density in angiosperm-dominated lowland and lower montane tropical forests is less well understood.

There have been few major ecological studies that focused on podocarp species in the Malesian region. The limited information presented here is obtained from a variety of published and unpublished sources, and it deals mostly with forest composition and structure in general or focuses on how our knowledge of podocarp ecology in temperate forests or of other tropical plant groups with some shared attributes (e.g., rarity) informs a growing understanding of their ecology.

DISTRIBUTION AND ECOLOGY OF MALESIAN PODOCARPS

Podocarps are typically infrequent components of lowland and lower montane tropical forests, but may strongly dominate in upper montane forests, alpine shrublands, and some swamp forest associations at both low and high elevations (Paijmans, 1976; Enright and Hill, 1995). Species of *Podocarpus*, *Nageia*, *Prumnopitys*, and *Sundacarpus* (with generally flattened, broad leaves) are most common in lowland and lower montane forests in Australia, New Guinea, and Southeast Asia, whereas those of *Dacrydium*, *Dacrycarpus*, and *Falcatifolium* (with generally imbricate/small leaves) are most common in higher-elevation forests of New Guinea and the Indonesian and Philippine islands. *Podocarpus* and *Dacrydium* species are also locally common in lowland peat and heath forests in Sarawak and Borneo (Whitmore, 1984; Nishimura et al., 2007). New Caledonia represents such a unique set of circumstances in terms of its isolation history, ultramafic geology, and associated vegetation assemblages (Jaffré, 1993) that its rich and wholly endemic podocarp flora is treated separately here.

WIDESPREAD AND COMMON SPECIES

Three species stand out in terms of their distributions, both geographically and altitudinally, through the

Malesian region: *Dacrycarpus imbricatus* is widespread in montane forests (500–3,000 m) from Fiji to northern Myanmar, *Podocarpus neriifolius* occurs in lowland to montane forests from Fiji to Nepal, and *Nageia wallichiana* occurs from India to New Guinea and the Philippines, mostly in lower montane and montane forests, but occasionally also in lowland stands close to sea level (Kuang et al., 2006; Thomas et al., 2007; see Appendix, Table 4.A1). *Podocarpus neriifolius* is exploited for timber and has been depleted in some regions, especially in low- and middle-altitude forests. Other species with wide geographic distributions include *Sundacarpus amarus* (northeastern Australia to the Philippines), *Podocarpus pilgeri* (Solomon Islands to southern China), and *Dacrydium beccarii* and *D. xanthandrum* (Solomon Islands to the Philippines). Although not necessarily widespread, some podocarps may be abundant within their geographic ranges, dominating the forest stands in which they occur. For example, *Dacrycarpus compactus* occurs only in New Guinea but is the principal tree line species there. It is present on almost all mountains of the central mountain chain, often as the tree line dominant. However, it is virtually absent from sandstone mountains (e.g., Mount Jaya) where *Papuacedrus papuana* (Cupressaceae) and *Phyllocladus hypophyllum* dominate (Hope, 1976). A range of podocarps is locally abundant on poor soils associated with ultramafic geology (e.g., *Podocarpus gibbsiae* and *P. confertus* in Borneo) and other resource-limiting substrates (e.g., *Dacrydium cornwallianum* in montane swamp forests in New Guinea and *D. pectinatum* in lowland heath and peat forests on acid sands in Borneo).

RARE AND RESTRICTED SPECIES

Among 85 species from 10 genera in the Malesian region outside of New Caledonia, 45 show geographic ranges restricted to a single country or island (Appendix). There are at least six endangered podocarps, and a further seven species are known from only one or a few collection sites. In Fiji, a number of narrow endemic taxa, including *Acmopyle sahniana* (critically endangered), *Dacrydium nausoriense* (endangered), and *Podocarpus affinis*, occur in small stands in cloud forest on ridgetops at 375–900 m. *Acmopyle sahniana* is restricted to three small stands at Namosi, Viti Levu. Populations are declining, seed production is poor, and there is no recent evidence of germination and recruitment of seedlings. In Tonga, the endemic *P. pallidus* occurs on steep slopes in *Calophyllum*- and *Garcinia*-dominated montane forest at 190–300 m on ‘Eua, one of the oldest (Eocene) and largest limestone

islands in the Tongan island chain (Drake, 1996). These isolated island species are threatened by logging and associated erosion, and little detailed information is available about the ecology of the podocarps growing there.

Other endangered species include *Dacrydium comosum* in Peninsular Malaysia, *Nageia fleuryi* in mainland Southeast Asia, *Podocarpus costalis* in the Philippines and Taiwan, and *P. nakaii* in Taiwan (Appendix). A number of local endemics are restricted to one or a few localities in northern Borneo on or near Mount Kinabalu, including *Dacrycarpus kinabaluensis*, *Podocarpus gibbsiae*, *P. globulus*, and *Falcatifolium angustum* (Sarawak), or to single mountains in New Guinea (*Dacrydium leptophyllum*, *D. spathoides*) or the Philippines (*Podocarpus lophatus*).

ALTITUDINAL ZONATION AND HIGH-ALTITUDE STANDS

Johns (1982) describes a generalized altitudinal forest zonation for New Guinea, with *Podocarpus* species often present at low density in angiosperm-dominated lowland (0–700 m) and lower montane rainforest (700–1,800 m), *Podocarpus* and *Dacrydium* present in *Nothofagus*-dominated mid-montane forests (1,800–3,000 m), and *Dacrycarpus* (with *Papuacedrus*; Cupressaceae) dominant near the tree line at altitudes of 3,000–3,900 m. Similar sequences can be described for other parts of Malesia, although mountain forest zones and altitudinal tree lines tend to occur at lower altitudes on smaller land masses and mountain ranges (the mass elevation effect), so that it is difficult to compare directly species’ altitudinal ranges among species and locations. Several podocarp species also occur above the tree line as shrubs in alpine scrub, including *Dacrycarpus kinabaluensis* on Borneo, *Dacrydium medium* in Sumatra, *Podocarpus spathoides* in Peninsular Malaysia, and *Dacrycarpus imbricatus* and *Podocarpus pilgeri* in central Irian Jaya (west New Guinea), where they form dense thickets 1–2 m high on infertile sandstone sites at 3,000 m (G. Hope, Australian National University, Canberra, Australia, personal communication).

Wade and McVean (1969) describe the high mountain forests of Mount Wilhelm, the highest peak in Papua New Guinea (4,510 m above sea level (asl)), in some detail: *Dacrycarpus cinctus* is prominent in *Nothofagus*-dominated montane forests at 2,400–2,800 m, reaching a diameter at breast height (dbh) of >100 cm. In mountain “cloud” forest at 3,100–3,350 m emergent podocarps (*Dacrycarpus compactus* and *Podocarpus pilgeri*) form an open canopy at around 25 m over a diverse angiosperm tree canopy (containing at least 44 species) at about 18 m. Seedlings and saplings of the tree species are abundant

in the understory, which is draped in bryophytes and filmy ferns. Associated species are primarily derived from groups with tropical affinity. However, with increasing altitude, a greater number of the forest species show affinity with either southern or northern temperate-latitude taxa.

Lower subalpine forest extends upward to about 3,600 m (Wade and McVean, 1969). These forests are lower (9–15 m) and structurally and floristically less complex (~35 tree species). Trees are often crooked, and few exceed 20 cm dbh, apart from the emergent *Dacrycarpus compactus*. *Gleichenia bolanica* and bryophytes may form thickets that exclude woody plants from the forest floor. The upper subalpine (tree line) forests on Mount Wilhelm occasionally reach 3,900 m, interfingering with alpine grasslands. *Dacrycarpus compactus* and *Rapanea vaccinioides* are emergent above a low tree canopy (6–12 m) containing a total of only 15 tree species. Woody shrubs from the Ericaceae are abundant in the understory.

Kitayama (1992) and Aiba and Kitayama (1999) describe altitudinal zonation of vegetation on Mount Kinabalu, Borneo, with patterns differing between ultramafic and nonultramafic substrates. In general, Kitayama (1992) identified four forest zones: lowland forests to 1,200 m, montane forests to 2,000 m, upper montane forests to 2,850 m, and subalpine forests to the tree line at 3,400 m. *Dacrycarpus imbricatus*, *Dacrydium pectinatum*, and *Falcatifolium falciforme* are prominent components of montane forest (at 1,560 m) on Tertiary sedimentary substrates, with densities of 20–50 trees >10 cm dbh per hectare (Aiba et al., 2004). *Falcatifolium falciforme* shows moderate abundance of small trees and saplings in the shaded understory, but juveniles of *Dacrycarpus* and *Dacrydium* are infrequent and appear to be associated with canopy openings. Forest structure and composition diverge markedly in the upper montane forest zone: forests on ultramafic substrate are of smaller stature and are dominated by *Dacrycarpus kinabaluensis* and the ultramafic endemic *Dacrydium gibbsiae*, whereas forests on nonultramafic substrate are dominated by angiosperm tree species. Podocarps (particularly *D. kinabaluensis*) become more prominent in subalpine forest on nonultramafic substrate, whereas they decline in abundance on ultramafic sites and are replaced there by dense, low (to 6 m) stands of *Leptospermum recurvum* (Myrtaceae). See Kitayama et al. (this volume) for more detailed coverage of the altitudinal vegetation sequence and factors affecting the distribution of podocarps on Mount Kinabalu. Detailed analyses of forest structure and composition in relation to altitude are lacking for many other parts of the region.

LOWLAND RAINFOREST

Podocarps are rare in the tropical lowlands. *Podocarpus neriifolius*, *Nageia wallichiana*, *N. motleyi* (Malaysia), *N. fleuryi* (Vietnam), and *Sundacarpus amarus* (northeastern Australia) are large trees (to 40 m height and >100 cm dbh) that tend to occur as solitary canopy trees in angiosperm-dominated lowland and lower montane forests. Seedlings and saplings are infrequent. Extensive prelogging surveys of lower montane (700–1,500 m asl) rainforests in the Bulolo and Jimmi Valleys of Papua New Guinea conducted in the 1940s and 1950s reported densities of 0–2 canopy trees >50 cm dbh per hectare for *P. neriifolius* and *S. amarus* (Papua New Guinea Department of Forests, unpublished reports). In a sample of 32 half-hectare plots in lower montane forest enumerated in the 1970s near Bulolo, Papua New Guinea, and dominated by either *Araucaria*, *Castanopsis*, or *Lithocarpus* (Fagaceae) species, podocarps were present in 10, mostly at densities of 2–4 individuals >10 cm dbh per hectare (N. Enright and R. Johns, Bulolo Forestry College, Papua New Guinea, unpublished data). A single outlier plot contained 16 individuals (32 ha⁻¹), evenly split between *P. neriifolius* and *S. amarus*, comprising ~12.5% of stand density and basal area. Although densities are too low to allow spatial analysis, the two species appear to occupy separate regions of the sample space and are not well mixed.

In a large rainforest census plot in the Pasoh Forest Reserve, Peninsular Malaysia (80 m asl), 27 trees of *N. motleyi* >1 cm dbh were recorded in a 50 ha plot containing >300,000 trees, and in a plot in Lambir Hills National Park, Sarawak, three trees were recorded in a sample of about 350,000 individuals in the forest overall at 100–200 m asl (<http://www.ctfs.si.edu>). *Podocarpus neriifolius* is also listed as a “frequent” canopy tree in rainforest on sandstones of the McHenry Uplands of Cape York Peninsula (11°S–12°S) in far northern Queensland, Australia (Adam, 1992). These species have among the largest leaves of any podocarp, along with *P. dispersum*, a geographically restricted species growing in the understory of wet forests in northeast Queensland between 16°30’S and 17°50’S.

HEATH AND SWAMP FORESTS

Heath (kerangas) and peat (kerapah) forests form on low-nutrient acidic sands and wet peaty soils, respectively, most commonly at low altitude in Borneo, Sumatra, and Malaya (Bruenig, 1990). They are characterized by

at least seasonal waterlogging and low levels of mineral nutrient availability and support high stem densities of small-diameter trees (typically <20 cm dbh) with smaller leaf size and markedly different floristic composition than lowland dipterocarp rainforest on nearby red-yellow clay soils (Oxisols and Ultisols) (Whitmore, 1984; Newbery et al., 1986). Drought stress is thought to be a major driver of forest structure and composition, with shallow root systems (a response to seasonal waterlogging) leading to increased vulnerability during dry periods. Miyamoto et al. (2007) reported a marked decrease in stand productivity during the El Niño drought of 1997–1998, followed by rapid return to much higher rates of biomass production, with overall rates similar to lowland dipterocarp forests. They concluded that a combination of high leaf mass allocation, small specific leaf area (as well as low leaf stomatal density and thicker/multiple palisade layers; Cao, 2000), and long leaf life span relative to adjacent lowland dipterocarp forest stands on more-fertile soils facilitated the maintenance of moderate levels of stand productivity under conditions of recurrent drought stress. Tyree et al. (1998) found no evidence of increased resistance to xylem cavitation/embolism among heath forest tree species, so that adaptation to drought appears primarily through leaf attributes. Nutrient deficiency, antiherbivore defenses, and heat load have also been suggested as factors that may interact with drought to explain the structure and dynamics of these forest types (Whitmore, 1984; Miyamoto et al., 2007). Riswan and Kartawinata (1991) reported much higher levels of recovery through vegetative resprouting (rather than seedling recruitment) following canopy disturbance relative to nearby dipterocarp forest, which may also be linked to water- and nutrient-related stress tolerance attributes of heath forest species.

Given these attributes, conifers might be expected to be generally more abundant in heath and swamp forests than in dipterocarp forest, and this is, indeed, the case. *Agathis borneensis* (Araucariaceae) is widespread and often dominant, and some of the highest-density stands of podocarps in the region also occur in heath forests. For example, Newbery (1991) recorded 40–72 *Podocarpus neriifolius* trees >7.6 cm dbh ha⁻¹ (but low basal area of 0.12–0.40 m² ha⁻¹) in heath forests in Sarawak and Brunei codominated by the dipterocarps *Shorea ovata* and *S. revoluta*, and Nishimua et al. (2007) reported 20 trees >5 cm dbh (but relative basal area of only 0.19%) for *N. wallichiana* in a 1 ha heath forest plot near Palangkaraya, Kalimantan. Although there are no data on recruitment or mortality rates, stem diameter growth rate over two years

was similar to or greater than that for most co-occurring angiosperm tree species (Nishimua et al., 2007). A number of other podocarps occur in heath and peat swamp forests in Borneo, including *Dacrydium pectinatum*, *Nageia maxima*, *Podocarpus laubenfelsii*, and *Sundacarpus amarus*. The higher-than-expected colonization of roots by arbuscular mycorrhizal fungi (relative to ectomycorrhizal fungi) in the surface organic soils of heath and swamp forests compared with mixed dipterocarp forest (Moyersoen et al., 2001) may be linked to the higher density of conifers, all of which have arbuscular mycorrhizal symbionts.

Podocarp dominance in swamp forest stands also occurs at some mid-montane elevations (1,400–2,300 m) in New Guinea. Several *Dacrydium* species (especially *D. nidulum*, but also *D. cornwallianum*) occur in almost pure stands (>95% of all trees) on swampy land in the Western and Southern Highlands. Associated species there include *Nothofagus grandis* and *Pandanus* sp. (Johns, 1976).

Members of the Podocarpaceae cover the whole geographic and altitudinal range occupied by forests in the Malesian region. Nevertheless, there is a strong tendency for dominance to be restricted either to high-altitude sites close to the limit of tree growth or to other sites that might restrict plant growth in terms of water relations or nutrient supply (e.g., steep slopes and ridges, heath and swamp forest formations, ultramafic geology, limestone hills, other infertile parent material, and skeletal soils). There is surprisingly little specific ecological information available for podocarps in lowland forest, probably because the extremely low density of trees makes field studies of demographic behavior difficult and unrewarding relative to the opportunities afforded by the many more abundant co-occurring (and sometimes commercially important) tree species.

DISTRIBUTION AND ECOLOGY OF NEW CALEDONIAN PODOCARPS

New Caledonia is distinctive in its podocarp flora, sharing no species with any other part of the region and with most species restricted to ultramafic substrates with unusual chemical properties. The Podocarpaceae of New Caledonia comprises 20 species in 8 genera: *Podocarpus* (9 spp.), *Dacrydium* (4 spp.), *Retrophyllum* (2 spp.), *Prumnopitys*, *Falcatifolium*, *Dacrycarpus*, *Acmopyle*, and *Parasitaxus* (Table 4.1). All species and one genus (*Parasitaxus*) are endemic (Appendix). They include shrubs, small trees, and trees (Figure 4.2). *Retrophyllum comptonii* reaches a

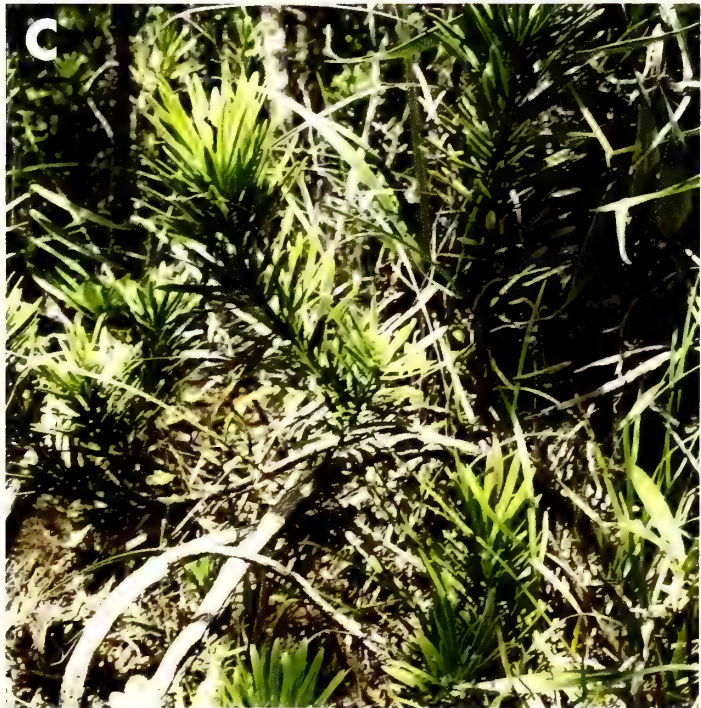




FIGURE 4.2. Examples of podocarps endemic to New Caledonia. *Facing page:* (A) *Parasitaxus usta*, the only known parasitic gymnosperm; (B) *Retrophyllum minus*, an endangered species restricted to permanent and ephemeral stream banks in the south of the Grand Terre; (C) *Podocarpus decumbens*, a critically endangered, sometimes lianescent, species restricted to high-altitude maquis on the summit of the Montagne des Sources in the south of the Grand Terre. *Above:* (D) *Acmopyle pancheri*, a widely distributed tree species of forests from 150 to 1000 m asl; (E) *Podocarpus novae-caledoniae*, a shrub species of low-altitude (0–700 m asl) ligno-herbaceous maquis in the south of the Grand Terre; (F) *Dacrydium guillauminii*, a critically endangered species restricted to a few streambank locations in the Plain of Lakes region in the south of the Grand Terre.

height of 30 m, and individuals 20–25 m high have been observed for *Dacrydium lycopodioides*, both species occurring in the canopy layer of dense evergreen rainforest. *Acmopyle pancheri*, *Dacrycarpus vieillardii*, *Dacrydium balansae*, *Falcatifolium taxoides*, *Podocarpus longefoliolatus*, *P. polyspermus*, *P. lucienii*, and *Prumnopitys ferruginoides* may reach 10–15 m but are usually shorter. Most occur in stunted montane rainforest at altitudes >1,000 m, except *D. vieillardii* (100–800 m), *D. balansae* (150–900 m), and *Podocarpus polyspermus* (650–950 m). *Dacrydium guillauminii* and *Retrophyllum minus*, reaching heights of 1–6 m, are restricted to river and lake edges in the south of the main island on ultramafic substrates. *Podocarpus novae-caledoniae*, *P. gnidioides*, *P. decumbens*, and *Parasitaxus usta* do not exceed 2 m in height. *Podocarpus decumbens* tends to be lianescent, whereas *P. gnidioides* has a prostrate habit when growing in exposed sites (Jaffré, 1995).

The overall distribution of podocarps in New Caledonia accords less with the archaic angiosperms than with the more advanced angiosperms. Grandcolas et al. (2008) reviewed recent geological and phylogenetic work on New Caledonian plants and animals and concluded that many groups, including the podocarps, most likely arrived by long-distance dispersal after 37 MYA, following up to 20 million years of total submersion of the main land mass, with little chance of survival in situ for Gondwanan stock. Low gene sequence divergence rates within the New Caledonian species of *Retrophyllum* reported by Herbert et al. (2002) support this view. Further, most new, locally endemic species within this (and other) taxa appear to have arisen over the last few million years, primarily in response to the major climatic fluctuations associated with glacial-interglacial cycles.

VEGETATION TYPES AND SPECIES DISTRIBUTIONS

Although only reaching a maximum elevation of about 1,600 m asl, the mountains of New Caledonia are characterized by montane cloud forest above 900 m similar in structure to forests at higher altitude (typically >2,000 m) on larger land masses such as New Guinea (Nasi et al., 2002). Annual rainfall exceeds 3,500 mm, and the vegetation is distinctly shorter than at lower altitudes, comprising a broken canopy layer of small trees with poorly developed trunks to 8 m high. The flora is less rich in angiosperms, although several species of the genera *Metrosideros* (Myrtaceae), *Cunonia*, and *Pancheria* (Cunoniaceae) are prominent, and genera with primitive features (*Nemuaron*, *Paracryphia*, *Quintinia*, *Sphenostemon*,

Trimenia, *Zygogynum*) are well represented, including the endemic family Phellinaceae. Podocarps are frequent in and beneath the low and discontinuous canopy, although many have fragmented distributions. *Retrophyllum comptonii* and *Dacrydium lycopodioides* contribute to the canopy of the forest or are emergent above it. *Dacrydium lycopodioides* is confined to exposed summits, whereas the more widespread *Retrophyllum comptonii* occupies a variety of sites. The extremely rare *Podocarpus longefoliolatus* (recorded from six localities on crests) is confined exclusively to the undergrowth of higher-altitude forests. *Acmopyle pancheri*, *Falcatifolium taxoides*, *Parasitaxus usta*, *Podocarpus lucienii*, *P. sylvestris*, and *Prumnopitys ferruginoides* have a wide altitudinal distribution between 150 and >1,000 m asl. Two podocarps are restricted to evergreen rainforest of low altitudes, *Dacrycarpus vieillardii* to gallery forests on alluvium subject to flooding and *Podocarpus polyspermus* on slopes mostly above 600 m and, less frequently, in gallery forest at 50 m asl. *Podocarpus novae-caledoniae* and *P. gnidioides* occur in ligno-herbaceous (sedge) maquis, the latter restricted to a few localized populations on rocky or lateritic crests.

Podocarps are rarely dominant, but *Dacrydium balansae* forms an almost pure canopy layer in forest on the massif of Koniambo between 400 and 600 m (perhaps suggesting cohort recruitment after landscape-scale disturbance), and *D. araucarioides* is an abundant species in shrubby secondary maquis often codominated by *Gymnostoma deplancheanum* (Casuarinaceae). *Dacrydium araucarioides* is a fire-killed, small tree to 20 cm dbh in low-altitude (mostly 100–400 m asl, but also in one locality at 900 m at Montagne des Sources), open-maquis vegetation on shallow soils and lateritic boulder fields (cuirasse ferralitique) derived from ultramafic parent material. McCoy (1998) and McCoy et al. (1999) found that growth rings were clear and probably annual, with counts suggesting ages of up to 125 years for individuals approaching 20 cm dbh. *Dacrydium araucarioides* may recruit continuously in dry, open forests with *G. deplancheanum* prominent, but recruitment declines in more-mesic sites as rainforest tree species form a closed canopy, with disturbance (e.g., by fire) needed for recruitment to resume.

Dacrydium guillauminii and *Retrophyllum minus* are confined to river margins and marshes in the southern ultramafic massif of the Grande Terre, in the Plain of Lakes region. The former is limited to four localities on the margins of the Rivière des Lacs and at the edge of the Lac en Huit. The latter grows at the margins of some other watercourses and, more rarely, on lateritic duricrust in shallow, periodically flooded depressions. Both species form

populations of a few to several dozen individuals, which are shrinking as a result of increased fire frequency and other human impacts, with population size of *R. minus* < 2,500 (Farjon and Page, 1999; Herbert et al., 2002) and considerably smaller for *D. guillauminii*. Although seed production and germination is good, seedling establishment beyond the perimeter of existing parent populations is very rare. Two other species, *Dacrycarpus vieillardii* and *Podocarpus novae-caledoniae*, also grow along stream banks and tolerate temporary inundation.

Parasitaxus usta is the only known parasitic conifer. Its foliage is red-purple, and it is always associated with *Falcatifolium taxoides*, from which it obtains nourishment by means of haustoria penetrating the base of the trunk or the roots (Köpke et al., 1981). Feild and Brodribb (2005) recently demonstrated that *P. usta* does not photosynthesize, has a strong connection of tracheids between its roots and those of *F. taxoides*, and is mycoheterotrophic—in combination, a unique solution to the parasitic life-form. It occurs around 1,000 m asl in mixed-angiosperm montane forests to 20 m high, with occasional emergent *Araucaria* to 30 m (and at a few locations in forests below 300 m in the south of the Grande Terre). Seeds are produced, but there has been little success in ex situ germination, and seedlings are infrequent. There are no data on stem growth rates or estimates of longevity, but on average, longevity must be less than that of its host plant *F. taxoides*, so perhaps up to 200 years.

ENVIRONMENTAL CONTROLS

All of the New Caledonian podocarps are either restricted to ultramafic substrates (which cover about one-third of the Grand Terre, mostly in the south) or occur on both ultramafic and nonultramafic (mostly metamorphic) parent materials. Soils derived from ultramafic rocks are characterized by low concentrations of nitrogen, phosphorus, potassium, and calcium. Only *Dacrydium balansae* is able to grow on hypermagnesium soils, in which a deficit in exchangeable calcium (<2 meq 100 g⁻¹) is accentuated by the antagonistic action of magnesium (Jaffré, 1980). On the other hand, many conifers grow on colluvial or eroded soils (often covered with a thick organic horizon at higher altitudes) characterized by a less-marked calcium/magnesium disequilibrium and greater concentrations of available nickel (>0.5%) and manganese in acidic soils. Analysis of mineral elements in chlorophyll tissues reveals a limited requirement for nitrogen, phosphorus, and potassium, as well as a capacity to selectively absorb calcium while limiting the absorption of manganese and nickel.

Root nodules are present, but no research has been conducted into their form for New Caledonian species or the role that they might play in mediating (or restricting) element uptake from soil.

The podocarps are mostly found in very wet environments (in dense rainforest, at higher altitudes, and at the margins of watercourses) and on ultramafic geology. They are usually light demanding, overtopping dense rainforests, or contributing to the dominant stratum of the maquis. They are also adapted to a wide range of habitats. Their affinity for ultramafic rocks probably results from their preadaptation to infertile soils and rocky sites, their apparent tolerance of sometimes toxic concentrations of nickel and manganese, and their light-demanding nature. In addition, the ultramafic substrate may limit the growth of some angiosperm groups, preventing the establishment of more rapidly growing species that have a high demand for nitrogen and phosphorus.

CONSERVATION AND THREATS

The rarest podocarps undoubtedly formerly occupied much larger areas but are now restricted to sites in wet montane forest on ridges (*Podocarpus decumbens*, critically endangered, and *P. longefolialis*, endangered) or along the margins of watercourses (*Dacrydium guillauminii*, *Retrophyllum minus*), which have provided them with a refuge from fire. The main populations of *Dacrydium guillauminii* (critically endangered) and *Retrophyllum minus* (endangered) are now protected within botanical reserves. However, mining activities in the region, leading to possible dewatering of soil profiles near intermittent watercourses, continue to be a potential threat to the survival of some populations (Pascal et al., 2008).

Perhaps among the most threatened species are the recently described *Podocarpus beecherae* (critically endangered, closely related to *P. novae-caledoniae*) from hilltop maquis in the south of the Grand Terre (de Laubenfels, 2003) and *P. colliculatus* (endangered) from a single locality in moist forest on ultramafic substrate at Pic N'ga, Île des Pins, where tourism is developing without adequate control (de Laubenfels, 2005). However, the taxonomic status of *P. colliculatus* remains to be officially confirmed, and this collection may be synonymous with *P. sylvestris* (T. Jaffré, personal observations). In contrast, conifers common in dense rainforest, such as *Falcatifolium taxoides*, *Prumnopitys ferruginoides*, and *Retrophyllum comptonii*, as well as some less-common species with a wide distribution (e.g., *Acropyle pancheri*) show less evidence of decline within the broad-leaved forests, although

post-European settlement fragmentation, logging, fire, and road construction (including many mining exploration and recreational tracks) have certainly had some impact; *A. pancheri* has been revised recently to nearly threatened. Now listed as vulnerable, *Parasitaxus usta*, the only known parasitic conifer, also seems to be disappearing from some formerly occupied sites. The potentially deleterious genetic consequences of fragmentation and population contraction in New Caledonian conifers have been illustrated for the rare *Araucaria nemorosa*, with genetic diversity lower in recent recruits than in parents and inbreeding becoming more common (Kettle et al., 2007). For the species of high-altitude, wet montane forests, global warming also poses a real threat that could cause the disappearance of their very specific ecological requirements (Nasi et al., 2002).

LIFE HISTORY ATTRIBUTES AND POPULATION ECOLOGY

Insights into the ecology of the Malesian podocarps may be gleaned from a consideration of their morphological and physiological attributes and comparison with those of co-occurring angiosperm tree species. For the majority of attributes little detail is known for these tropical podocarps relative to their temperate relatives. Nevertheless, some generalizations can be made and areas for fruitful future investigation identified.

ECOPHYSIOLOGY

Brodribb and Hill (1998, 1999, 2004) and Brodribb et al. (2005) have established a detailed understanding of the ecophysiological responses of podocarp seedlings for a mix of both temperate and tropical taxa that informs our understanding of their growth and survival in the understory of lowland mixed angiosperm–conifer forests. Most species have evolved bilaterally flattened leaves that mimic angiosperm leaves in shape and are efficient in the low-light environment of the forest understory. However, other than in the genus *Nageia*, podocarp leaves are single-veined, and this may set limits to leaf size and hydraulic conductivity that place them at a disadvantage relative to angiosperm tree species. On the basis of a broad survey of podocarp distributions in relation to climate and water availability, Brodribb and Hill (1998) concluded that podocarps were more constrained by seasonal drought than by overall patterns of rainfall, so that species were largely confined to moist, aseasonal or

weakly seasonal climates. Brodribb et al. (2005) showed that seedlings of two tropical Malesian understory podocarps (*N. fleuryi* and *P. grayae*) had sixfold lower growth than comparison angiosperms under high-light conditions (1,300–1,800 mmol s⁻¹), whereas at low light levels (30 mmol s⁻¹) growth rates were more similar but still significantly lower. The podocarps consistently had lower leaf to stem ratios (i.e., were constrained to support more nonphotosynthetic tissue) and were slower to respond to increases in light. Ultimately, the authors concluded that these tropical podocarps had lower rates of gas exchange and less-efficient production of leaf area than angiosperms and were best able to compete with angiosperms as stress tolerators under low light, where their disadvantage was at a minimum. Despite multiple veins per leaf, species of (the more recently evolved) *Nageia* are not clearly more successful than other forest podocarps.

Similar results were reported by Rundel et al. (2001), who found very low rates of net photosynthesis in *N. wallichiana* under high-light conditions in Thailand, and by Pammenter et al. (2004) in relation to hydraulic properties of angiosperms and conifers, including *Podocarpus latifolius*, in southern Africa. Pammenter et al. (2004) further concluded that the competitive advantage to angiosperms was maximized under high-productivity circumstances, with conifer competitiveness less impacted under low-soil-nutrient (e.g. see Becker, 2000) and low-light conditions, such as in cloud forest, where both canopy and atmospheric factors contribute to low light availability.

POPULATION ECOLOGY

Many podocarps, especially in the genus *Podocarpus*, are dioecious, and all have wind-dispersed pollen, traits that may lead to the generally low tree densities reported for them in lowland tropical forests. Pollen dispersed by wind must fortuitously find its way from male to female plants across a landscape filled with competing species, whereas seeds (and seedlings recruited from them) can only be produced and dispersed from female adults, so that sex ratios and spatial distributions of adults also become important components of the species dynamics. Indeed, Haig and Westoby (1991) and Regal (1977) argued that the cost of rarity in angiosperms was lower than that in conifers because of the advantages of efficient insect and bird pollination relative to inefficient wind pollination. To what extent the combination of dioecy and wind pollination occurs in rainforest tree floras is unknown, but it may be infrequent; for example, Behling et al. (1997) reported that *Podocarpus lambertii* was the only wind-pollinated

species among 97 tree species in a 1 ha plot in southern Atlantic rainforest in Brazil. Nanami et al. (2005) investigated the sex ratio in the Japanese podocarp *Nageia nagi*, finding a bias in the number of males, faster growth rate in males, and spatial segregation between male and female adults. Female trees were also more heavily impacted by neighbor competition. No similar studies have been conducted for podocarps in tropical forests.

Podocarp seeds are dispersed by birds, and perhaps some small mammals, which are attracted by the typically single-seeded fleshy fruit and/or swollen bract. Fruiting structures range from green to red or purple in color. Seed production varies considerably among species, being recorded as infrequent or even rare in some cases (e.g., *P. neriifolius* in Vietnam). Germination of tropical podocarp species is usually rapid, ranging from 20 to 60 days for *Dacrycarpus imbricatus*, *Nageia fleuryi*, and *P. neriifolius*, with seeds then losing viability so that there is no persistent soil-stored seed bank. Baskin and Baskin (2001) noted that the widespread and common *Dacrycarpus imbricatus* and *Podocarpus neriifolius* exhibit morphological dormancy (underdeveloped embryos at time of dispersal) but that germination can occur within four weeks of dispersal, whereas the rare and endangered *Dacrydium comosum* exhibits morphophysiological dormancy, requiring both growth of the embryo to critical size and breakdown of physiological dormancy, thus slowing germination. Delayed seed germination, sometimes exceeding one year (Enright and Cameron, 1988; Geldenhuys, 1993), and a requirement for cold stratification have been reported for a number of temperate podocarps (Fountain and Outred, 1991) but are unlikely for tropical species. Seed germination ex situ has proven difficult in some other tropical species; for example, Doust et al. (2006) were unable to germinate cleaned seeds of *Sundacarpus amarus* in a study of rainforest restoration procedures in northeast Australia. This species is thought to be dispersed by the flightless cassowary, a tropical forest bird species now in significant decline due to forest fragmentation, logging, and other human impacts (Westcott et al., 2005). Cassowaries are considered to be important in the dispersal of >100 species of rainforest trees in northeast Australia and New Guinea, and their loss as a dispersal vector may seriously impact the future abundance and genetic structure of such species (Stocker and Irvine, 1983; Mack, 2006). Cordero and Howe (2002) documented significantly lower rates of seedling recruitment in plant species dependent upon fruit-eating animals for seed dispersal (relative to wind and gravity dispersal species) in small versus large forest fragments for a tropical submontane forest in Tanzania,

with primate and bird counts confirming frugivore species decline with decreasing fragment size.

Masting has been well documented for many temperate podocarps and is also likely among tropical species, especially given its occurrence in other tropical conifer taxa, such as *Araucaria*. Chalwell and Ladd (2005) suggested that synchronized high cone and pollen production years may be beneficial to dioecious understory plants (such as *Podocarpus drouynianus* in southwestern Australia; see Ladd and Enright, this volume), which are dependent upon wind dispersal of pollen in a low-wind environment. Although the tropical podocarps may be canopy trees, their low density provides a similar context within which one might argue that mast strobili and coning years would best ensure pollination of low-abundance, coning trees. However, parentage could be asymmetrical; female trees of both canopy and subcanopy size may receive pollen, but only canopy males may successfully disperse pollen to them if pollen dispersal in subcanopy males is limited by reduced atmospheric turbulence. Over what distances predominantly understory podocarps of closed forests successfully disperse pollen is unknown. Behling et al. (1987) measured pollen rain in traps distributed systematically through a 1 ha Atlantic rainforest plot in Brazil containing four *Podocarpus lambertii* trees. Pollen influx for the podocarps was generally low but highly variable across the plot, with distinctly higher values at two pollen trap sites (presumably close to pollen-producing trees). They concluded that pollen transport among rainforest trees can often be very limited and short distance.

In the absence of a persistent soil seed bank, potential recruits to the subcanopy, and eventually the canopy, of the forest must accumulate and persist in a seedling bank in the low-light environment of the forest understory. Data for size frequency distributions of podocarps in tropical forests are as infrequent as the species themselves and are generally restricted to individuals >5 cm dbh, so that there are no data for seedlings and small saplings. Aiba et al. (2004) reported size distributions (>5 cm dbh) for *Dacrycarpus imbricatus* and *Falcatifolium falciforme* in tropical montane forest at Mount Kinabalu, and in both cases the numbers in the smallest size class were smaller than those in some larger classes, suggesting relatively poor rates of recruitment in undisturbed forest. Elsewhere, Tesfaye et al. (2002) reported “hampered” regeneration in *Afrocarpus falcatus* in montane forests in Ethiopia based on size distribution studies, and Arriaga (2000) recorded *P. matudae* as a gap-phase species dependent upon disturbance for recruitment in tropical montane cloud forest at Tamaulipas, Mexico.

PERSISTENCE AND COEXISTENCE

Given the low density of many podocarp species in lowland rainforests, it is uncertain how they can persist with the large number of co-occurring tree species, many of which show higher levels of fecundity and faster growth rates under both high- and low-light conditions. This conundrum also applies to rare or infrequent angiosperm species. Rosetto and Kooyman (2005) found that persistence of the paleoendemic rainforest tree *Eidothea hardeniana* (Proteaceae) in a subtropical forest in northern New South Wales, Australia, was best explained by a combination of large and unpalatable fruits, on the one hand, and tolerance facilitated by basal resprouting, on the other. On the basis of a life history trait analysis of 258 local taxa, they concluded that these traits might explain the restricted distribution and rarity of a number of other locally endemic rainforest species.

Wright (2002) reviewed mechanisms for coexistence in tropical forests, identifying the lack of competition between suppressed understory plants as potentially important, and Russo et al. (2005) reported lower growth and mortality rates among trees on infertile soils in lowland Bornean rainforest, with increased cost of herbivory on resource-poor sites perhaps selecting for better-defended and slower-growing taxa, such as conifers. Indeed, among lowland forest sites, podocarps achieve their highest densities in low-nutrient swamp and heath forests. These findings suggest that podocarp populations in angiosperm-dominated rainforests are best viewed as stress tolerators, characterized by slow growth rate and low mortality rate (but also low levels of herbivore damage), largely avoiding competition with faster-growing species through their location on low-nutrient sites and in deep shade, where angiosperm competitiveness is reduced most strongly.

Although the development of dense podocarp and other conifer species stands in montane forests may be associated with large-scale disturbance by storms and fire (e.g., see Enright et al., 1999, on araucarian forest stand dynamics in the Southwest Pacific region), the ultimate growth of low-abundance podocarps to the canopy layer in lowland tropical forests most likely depends upon canopy gaps caused by the death of individual trees. However, ecophysiological evidence suggests that angiosperm competitors should be greatly advantaged by any sudden increase in light availability (e.g., Brodribb et al., 2005) and would preempt such gaps. Thus, it may take several cycles of gap formation at a single location before the subcanopy podocarps are able to capture a canopy space, implying the need for markedly greater longevity than in co-occurring angiosperm species.

Indeed, longevity is one of the most obvious differences in life history traits between conifers and comparable angiosperm woody perennial species at a global scale. Loehle (1988) compiled typical and maximum life spans, time to reproduction, growth rate, and shade tolerance for a sample of 44 conifer and 76 angiosperm tree species from North America. These data revealed a median longevity of 250 years for angiosperms and 400 years for conifers. A list compiled for Southern Hemisphere conifers by Enright and Ogden (1995) revealed a strikingly similar distribution of maximum longevity but a higher median for conifers of 525 years, although some arid-zone conifers (e.g., *Callitris* species of semiarid woodlands in Australia) with longevity in the 100- to 300-year range were excluded from consideration. Little additional information of relevance has been published since this analysis. Data on stem diameter growth rate and maximum recorded tree size for three tropical podocarps from Mount Kinabalu (*Dacrycarpus imbricatus* and *Falcatifolium falciforme*; Aiba et al., 2004) and Kalimantan (*Nageia wallichiana*; Nishimura et al., 2007) suggest life spans of 400 years or more. Co-occurring angiosperm tree species growth rates and tree sizes suggest longevity ranging from less than 200 years to more than 400 years, so that although most angiosperm trees were shorter-lived, at least some were likely equally long-lived. Overall, data for forest podocarps suggest that tropical podocarp species of lowland and lower montane forests might have longevity in the 400- to 600-year range (Table 4.2).

Southern Hemisphere conifers also show very high nutrient use efficiency for nitrogen and phosphorus relative to most (but not all) angiosperm tree types (Enright and Ogden, 1995), although there is little specific evidence for podocarps. The ability to photosynthesize over a longer time period per unit of nutrient use (i.e., greater leaf longevity) and lower mean leaf nitrogen concentration may be the primary mechanism of increased use efficiency (Chapin, 1980; Enright and Ogden, 1987; Sprugel, 1989; Becker, 2000). Although very long leaf longevity have been shown for araucarians and some other conifer groups, little information is available on leaf longevity and nutrient levels for tropical podocarps relative to co-occurring angiosperm trees.

Another question relevant to the dynamics of some sparse, lower montane and lowland podocarp populations is the extent to which long-distance dispersal of seeds and pollen might operate to maintain (or rescue) populations that may otherwise decline and disappear. Some podocarp species of lowland forests are broadly distributed and are characterized by much greater population sizes

TABLE 4.2. Selected life history properties of Southern Hemisphere podocarps (modified from Enright and Ogden, 1995). Data are from Palmer and Pitman (1972), Ogden (1978,) Veblen et al. (1981), Ash (1985), Norton et al. (1988), Lusk and Ogden (1992), Enright et al. (1995), McCoy (1998), Aiba et al. (2004), and Nishimura et al. (2007).

Species	Location	Longevity (years)	Growth rate ^a	Shade tolerance ^b
<i>Afrocarpus falcatus</i>	South Africa	700	2	3
<i>Dacrycarpus dacrydioides</i>	New Zealand	600	1	2
<i>D. imbricatus</i>	Borneo	400 ^c	2	2
<i>Dacrydium araucarioides</i>	New Caledonia	200	1	1
<i>D. cupressinum</i>	New Zealand	1,160	2	3
<i>D. nidulum</i>	New Guinea	363	3	3
<i>Falcatifolium falciforme</i>	Borneo	400 ^c	1	3
<i>Nageia wallichiana</i>	Borneo	400 ^c	2	3
<i>Podocarpus hallii</i>	New Zealand	555	2	2
<i>P. latifolius</i>	South Africa	500	2	4
<i>P. lawrencei</i>	SE Australia	460	1	2
<i>P. nubigenus</i>	South America	400	3	3
<i>P. totara</i>	New Zealand	890	2	2
<i>Prumnopitys ferruginea</i>	New Zealand	771	1	4
<i>P. ladei</i>	SE Australia	600	2	3
<i>P. taxifolia</i>	New Zealand	1,013	1	2
<i>Saxegothaea conspicua</i>	South America	400	3	4

^a Scale: 1 = <1 mm year⁻¹, 2 = 1–2 mm year⁻¹, 3 = 2–3 mm year⁻¹.

^b Scale: 1 = intolerant (full light) to 4 = tolerant.

^c Longevities based on growth rate and stem diameter data.

and densities at higher altitudes or under specific habitat conditions (e.g., *Podocarpus neriifolius* occurs from sea level to 2,100 m, typically as scattered trees in lowland forests, but at increasing density at higher altitudes on dry ridgetops, on infertile soils), and it is not clear to what extent the dynamics of sparse lowland populations might be supported by inputs from higher-elevation populations or might rely upon local dynamics. The “rescue” hypothesis is supported by evidence from Behling et al. (1997), who reported pollination of a single individual of *Araucaria angustifolia* in Atlantic rainforest in Brazil from long-distance-transported pollen grains that must have come from a highland population at least 25 km away. This question could readily be addressed by using genetic methods to identify both mother (from nuclear microsatellite markers) and father (from chloroplast microsatellite markers) plants for each seedling/sapling/small tree encountered, so that the distribution of individuals in relation to pollen and seed dispersal could be analyzed. Such analyses would reveal dispersal distances and the extent to

which pollen and seed is derived within local populations (e.g., see Godoy and Jordano, 2001; Dick et al., 2003).

SYNTHESIS

The ecology of podocarps in tropical forests of New Caledonia and the Malesian region is massively understudied relative to that for their temperate counterparts in New Zealand, Tasmania, South Africa, and South America. This is particularly true for species present in low-density populations of lowland and lower montane angiosperm-dominated forests and reflects both the significant problems of studying low-abundance species in situ and the demand for scientific attention from the many competing (including more abundant and more economically important) species in these high-diversity ecosystems. Field studies of low-abundance tree species are difficult; trees are hard to locate (and to relocate), sample sizes are small, and study sites are large (and therefore often highly

heterogeneous), complicating data collection, analysis, and interpretation in relation to basic questions concerning their ecology and demography. Although some components of these species' life histories might be explored ex situ, including seed viability and germination and seedling growth/ecophysiology in relation to key environmental gradients (light, nutrients), and other information might be obtained from analyses of wood and leaf properties, most parts of their life histories (particularly pollen and seed dispersal, recruitment, growth and survivorship) must be examined in situ if we are to understand how and why they are able to persist at low density in angiosperm-dominated stands.

In this review we have sought to detail what is known about the distribution and ecology of podocarps in tropical and subtropical vegetation types of the Malesian region and why podocarp species are distributed in this way. A lack of data from field-based investigations means that conclusions about drivers of population dynamics often must be inferred using data from ex situ experiments on

seeds and seedlings and in situ studies for other (better studied) conifers and some angiosperm tree species characterized by (analogous) low density in tropical forests. Our conclusions largely support the hypotheses proposed by Midgley and Bond (1989) and Wright (2002) and the conclusions of experimental studies of seedling physiology by Brodribb and colleagues (Brodribb and Hill, 1998, 1999, 2004; Brodribb et al., 2005). Podocarps are often most abundant at sites where the growth of competing species is limited. However, their high species diversity in the Malesian region and the broad range of vegetation types and environments in which they are found suggest that they are a highly successful plant group that has adapted to a remarkably broad range of environmental conditions. Nevertheless, detailed field investigations of species demographies (including genetic marker studies of pollen and seed dispersal) are required urgently in order to establish a sound understanding of tropical podocarp ecology and to explain their population dynamics and the circumstances facilitating their recruitment and persistence.

APPENDIX

TABLE 4.A1. Podocarp species of the tropical and subtropical Malesian region. Data were compiled from de Laubenfels (1969, 1985, 1987, 1988, 2003, 2005), Silba (1986, 1987), Enright and Hill (1995), Farjon (2008), and the Gymnosperm Database, <http://www.conifers.org/index.html>.

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
<i>Acmopyle</i> Pilg.																								
<i>A. pancheri</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. sahniana</i> Buchh. & Gray	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dacrycarpus</i> (Endl.) de Laub.																								
<i>D. cinctus</i> (Pilg.) de Laub.	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. compactus</i> (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. cumingii</i> (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-	-
<i>D. expansus</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. imbricatus</i> (Blume) de Laub.	-	1	-	1	1	-	1	1	1	1	1	1	1	1	1	-	-	-	-	-	1	1	-	1
<i>D. kinabaluensis</i> (Wassch.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. steupii</i> (Wassch.) de Laub.	-	-	-	-	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. vieillardii</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dacrydium</i> Soland.																								
<i>D. araucarioides</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. balansae</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued)

TABLE 4.A1. (Continued)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
<i>D. beccarii</i> Parl.	-	-	-	-	1	-	1	1	1	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-
<i>D. comosum</i> Corner	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>D. cornwallianum</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. elatum</i> (Roxb.) Wallich	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	-	1	-	-	-	-	-	-	-
<i>D. ericoides</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. gibbsiae</i> Stapf.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. gracile</i> de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. guillauminii</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. leptophyllum</i> (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. lycopodioides</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. magnum</i> de Laub.	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. medium</i> de Laub.	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
<i>D. nausoriense</i> de Laub.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. nidulum</i> de Laub.	-	1	-	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. novo-guineense</i> Gibbs.	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. pectinatum</i> de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-
<i>D. spathoides</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>D. xanthandrum</i> Pilg.	-	-	-	-	1	-	1	-	1	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-
<i>Falcatifolium</i> de Laub.																								
<i>F. angustum</i> de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. falciforme</i> (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. gruezoii</i> de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>F. papuanum</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>F. taxoides</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nageia</i> Gaert.																								
<i>N. fleuryi</i> (Hickel) de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	1	-	-	-
<i>N. formosensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>N. maxima</i> (de Laub.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>N. motleyi</i> (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-	-	-	-	-	-
<i>N. nagi</i> (Thunb.) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
<i>N. wallichiana</i> (Presl.) O. Kuntze	-	-	-	-	-	-	1	1	1	1	1	1	1	-	-	1	-	1	1	-	1	1	-	1
<i>Parasitaxus</i> (Veillard)																								
<i>P. usta</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phyllocladus</i> L. C. et A. Rich																								
<i>P. hypophyllum</i>	-	-	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>Podocarpus</i> L. Herit. ex Pers.																								
<i>P. affinis</i> Seeman	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. annamiensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
<i>P. archiboldii</i> Gray	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. atjehensis</i> (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. beecherae</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued)

TABLE 4.A1. (Continued)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
<i>P. borneensis</i> de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. bracteatus</i> Blume	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. brassii</i> Pilg.	-	-	-	-	-	-	1	-	1	1	1	1	-	1	-	-	-	-	-	-	1	1	-	-
<i>P. brevifolius</i> (Stapf.) Foxw.	-	-	-	-	-	-	-	-	1	1	1	1	-	1	-	-	-	-	-	-	1	1	-	-
<i>P. chinensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
<i>P. chingianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>P. colliculatus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. confertus</i> de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. costalis</i> C. Presl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
<i>P. crassigemmis</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. decumbens</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. deflexus</i> Ridley	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
<i>P. degeneri</i> (Gray) de Laub.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. dispermus</i> White	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. elatus</i> R. Brown ex Endl.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. fasciculus</i> de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. gibbsiae</i> Gray	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. glaucus</i> Foxw.	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. globulus</i> de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. gnidioides</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. grayae</i> de Laub.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. insularis</i> de Laub.	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. laubenfelsii</i> Tiong	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. ledermannii</i> Pilg.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. levis</i> de Laub.	-	-	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. longefoliolatus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. lophatus</i> de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. lucienii</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. macrocarpus</i> de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. macrophyllus</i> (Thunb.) Sweet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1
<i>P. micropedunculatus</i> de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. nakaii</i> Hayata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. nerifolius</i> Don ex Lamb.	-	1	-	-	1	-	1	1	1	-	1	1	1	1	-	1	-	1	-	1	-	1	-	-
<i>P. novae-caledoniae</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. palawanensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. pallidus</i> Gray	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. pilgeri</i> Foxw.	-	-	-	-	1	-	1	1	1	-	1	-	-	-	-	1	1	-	-	-	1	1	-	-
<i>P. polyspermus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. polystachyus</i> R. Brown ex Endl.	-	-	-	-	-	-	1	1	-	1	-	1	-	-	-	1	-	-	-	-	-	1	-	-
<i>P. pseudobracteatus</i> de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. ridleyi</i> (Wassch.) Gray	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-

(continued)

TABLE 4.A1. (Continued)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
<i>P. rotundus</i> de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
<i>P. rubens</i> de Laub	-	-	-	-	-	-	1	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. rumphii</i> Blume	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
<i>P. salomoniensis</i> Wassch.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. smithii</i> de Laub.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. spathoides</i>	-	-	-	-	1	-	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>P. subtropicalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>P. sylvestris</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. teysmannii</i> Miquel	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
<i>Prumnopitys</i> Philippi																								
<i>P. ferruginoides</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. ladei</i> (Bailey) de Laub.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Retrophyllum</i> C. N. Page																								
<i>R. comptonii</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>R. minus</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>R. vitiense</i> (Seem.) C. N. Page	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sundacarpus</i> (Buchh. & Gray) C. N. Page																								
<i>S. amarus</i> (Blume) C. N. Page	-	-	-	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	1	-	-
TOTAL SPECIES	1	8	20	2	11	6	31	15	15	8	30	16	14	7	3	5	3	2	1	1	12	20	6	4
TOTAL GENERA	1	5	8	2	3	4	8	7	6	6	7	5	4	4	3	2	3	2	1	1	4	7	2	3

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Podocarps in Africa: Temperate Zone Relicts or Rainforest Survivors?

Hylton Adie and Michael J. Lawes

ABSTRACT. Podocarp distribution in Africa follows a discontinuous mountainous belt from Cameroon to Angola in the west and from Ethiopia in the northeast to the southern Cape in South Africa. Besides a relict population of *Afrocarpus falcatus* in coastal lowland forest in northeastern South Africa and southern Mozambique, African podocarps are generally limited to highland (Afrotemperate) regions. All podocarps are restricted to montane regions in Madagascar. Afrotemperate landscapes are characterized by a patchy mosaic of forest and grassland. Processes in the matrix, such as fire, are important drivers of forest distribution in the highland regions. Here we examine the relative performance of podocarps and angiosperms along an altitudinal gradient from temperate highlands to subtropical coastal regions in eastern South Africa. *Podocarpus latifolius* is a successful component of temperate highland forest, where it dominates old-growth stages. The success of podocarps is attributed to their greater longevity and ability to regenerate in shade, whereas many potential competing angiosperms are less capable of doing so. Regeneration by *P. latifolius* and associated angiosperms is less successful in high-light gap environments, where ferns and grasses suppress establishment. Podocarps are rare in coastal scarp forest, where the population is dominated by adult individuals. They are unable to regenerate in very deep shade (<3% daylight), which may account for the lack of *P. latifolius* regeneration beneath the dense canopy of coastal scarp forest. Low-nutrient soils did not favor podocarps over angiosperms, although the fact that soil nutrients do not appear to be limiting and the scarcity of shade-tolerant angiosperms in forests may influence this outcome. The relative role of light and soils on angiosperm-conifer competition is unknown for lowland forest, although current evidence from montane forests suggests that under prevailing soil conditions, light is the more important axis of niche differentiation.

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INTRODUCTION

The subtropical forests of southern Africa are characterized by a mixed angiosperm-*Podocarpus* composition that ranges along a productivity gradient from angiosperm dominance in coastal and mid-altitude (1,100–1,500 m above

sea level) forests to podocarp dominance in high-altitude montane forests. The dynamics of these main components are poorly understood, and mechanisms explaining their dominance have not been examined in detail (Adie and Lawes, 2009a). In temperate forests, the mechanisms conferring component dominance are proposed variously as climatic and soil nutrient constraints on angiosperm seedling growth rates in favor of slow-growing conifers at high altitudes (Bond, 1989), conifer shade tolerance (Midgley et al., 1990), a less-competitive reproductive system in terms of the ability of conifers to colonize or capture space relative to most angiosperms (Bond, 1989), competitive exclusion of podocarps by the understory vegetation, especially herbs and grasses in more productive environments (Midgley and Bond, 1989; Midgley et al., 1995a), prevention of shade-tolerant conifers from escaping angiosperm competition in deep shade (Coomes et al., 2005), and the intensity and frequency of large-scale disturbances (Ogden and Stewart, 1995; Ogden et al., 2005). In the Southern Hemisphere podocarps appear to have the competitive edge relative to associated angiosperms in seasonally colder temperate sites that experience periodic intense disturbance, and they are a successful component of montane forests in tropical latitudes but are rare in lowland tropical forests (Enright, 1995; Enright and Jaffré, this volume).

We examined the dynamics of high-altitude podocarps in the subtropics and focused on regeneration patterns of the two principal forest canopy components: conifers, represented by *Podocarpus latifolius*, and angiosperms (all other species). Angiosperms are reported to have poor regeneration in many inland forests (Moll, 1972; Everard et al., 1995; West et al., 2000; Lawes et al., 2007b), possibly due to shade intolerance (Midgley et al., 1995b). In a landmark paper, Bond (1989) explored factors limiting the distribution of conifers. He argued that faster-growing and competitively superior angiosperms outperform conifers in the early regeneration phase, restricting conifers to edaphically or climatically suboptimal sites. Bond's proposal continues to stimulate interest (Becker, 2000; Coomes et al., 2005). In this chapter we examine the question: What enables podocarps to persist in angiosperm-dominated environments? As an introduction to the African Podocarpaceae we briefly discuss the taxonomic status of African and Madagascan species. Next, we examine the historical biogeography of African Podocarpaceae and propose an explanation for distribution anomalies consistent with differences in dispersal and reproductive biology between podocarp taxa. Finally, we explore a case study that investigates the regeneration

ecology in eastern South African montane forests to understand the angiosperm–conifer contest.

TAXONOMY

Compared with the rest of the Southern Hemisphere, Africa and Madagascar are relatively depauperate in species belonging to the Podocarpaceae (Farjon, 2001; Mill, 2003). In this review we refer collectively to members of African Podocarpaceae as podocarps. Two genera (*Afrocarpus*, *Podocarpus*) and 13 to 17 species are recognized from the continent and associated islands (Table 5.1). All taxa were previously placed in the genus *Podocarpus* (for a recent review see Barker et al., 2004), but recent morphological (Kelch, 1997) and molecular (Kelch, 1998; Conran et al., 2000; Sinclair et al., 2002; Barker et al., 2004) data support the decision to raise the section *Afrocarpus* to generic level as proposed by Page (1989). *Afrocarpus* is more closely related to the podocarp genera *Nageia* (Southeast Asia, India, Japan, Philippines, Indonesia) and *Retrophyllum* (South America, Indonesia, New Caledonia) than to the rest of the African species incorporated into *Podocarpus* (Conran et al., 2000; Sinclair et al., 2002). The genus-level identity of podocarp pollen is confounded by the failure to separate *Podocarpus* from *Afrocarpus* in the pollen record. Where podocarps appear in West African pollen cores they are assumed to be *Podocarpus* because of the present West African distribution of the genus.

The present status of several podocarp taxa in Africa and Madagascar is uncertain. Dowsett-Lemaire and White (1990) adopt the view that the four podocarp species from South Africa (*A. falcatus*, *P. henkelii*, *P. latifolius*, *P. elongatus*) are the only true species on mainland Africa. In support of this notion, de Laubenfels (1985) considered *P. ensiculus* collected from the western Usambaras of Tanzania (Melville, 1954) to be a synonym of *P. henkelii*, endemic to the midlands of southeastern South Africa. More recently, the *henkelii-ensiculus* group has been recorded from the highlands of Malawi (Dowsett-Lemaire and White, 1990). Farjon (2001) recognizes differences between temperate southern Africa and tropical Africa by assigning the formerly pan-African species *A. falcatus* and *P. latifolius* to southern Africa and acknowledging *A. gracilior* from east Africa and the central African *P. milanjanus*, respectively. Using DNA sequence data, Barker et al. (2004) were unable to separate *P. milanjanus* from *P. latifolius*. These authors concede, however, that failure to detect sequence differences does not negate

TABLE 5.1. Podocarpaceae species from Africa and Madagascar (after Farjon, 2001).

Species	Broad distribution
<i>Afrocarpus dawei</i>	East African highlands (Kenya, Tanzania, Uganda, Democratic Republic of the Congo)
<i>Afrocarpus falcatus</i>	Southern South Africa (Swellendam) eastwards through highlands of Eastern Cape, KwaZulu-Natal, north into Mpumalanga and Northern Province, and into southern Mozambique (coastal)
<i>Afrocarpus gaussonii</i>	Eastern plateau of Madagascar
<i>Afrocarpus gracilior</i>	Highland regions of Ethiopia, Kenya, Tanzania, Uganda
<i>Afrocarpus mannii</i>	São Tomé Island in the Gulf of Guinea
<i>Afrocarpus usambarensis</i>	Burundi, Rwanda, Congo, Tanzania
<i>Podocarpus</i> (section <i>Podocarpus</i>)	
<i>Podocarpus elongatus</i>	Winter rainfall region of Western Cape, South Africa
<i>Podocarpus latifolius</i>	Southern South Africa (Swellendam) eastwards through highlands of Eastern Cape, KwaZulu-Natal, Mpumalanga, and Northern Province
<i>Podocarpus</i> (section <i>Scytopodium</i>)	
<i>Podocarpus capuronii</i>	Endemic to Madagascar, mountainous regions
<i>Podocarpus henkelii</i>	Highland regions of Eastern Cape and KwaZulu-Natal provinces of South Africa
<i>Podocarpus humbertii</i>	Endemic to Madagascar, mountainous regions in north
<i>Podocarpus madagascariensis</i>	Endemic to Madagascar
<i>Podocarpus rostratus</i>	Endemic to Madagascar, mountainous regions

species distinctness, given that morphologically distinct *A. falcatus* and *A. gracilior* have identical markers for the same region tested. In this review we consider *P. milanjanus* to be a synonym of *P. latifolius* (Drummond, 1975; Barker et al., 2004). In Madagascar, de Laubenfels (1985) proposed that *P. woltzii* and *P. perrieri* be synonymized within *P. capuronii* and *P. rostratus*, respectively. Stockey et al. (1998), however, comment that the rarity of some Madagascan podocarp species may have resulted in their incorporation into a single taxon. Using cuticle micromorphology, these authors found some evidence to split the *P. capuronii*–*P. woltzii* and *P. rostratus*–*P. perrieri* pairs into distinct species.

In Africa, all podocarp species occur in highland regions or, if coastal, then mostly at temperate latitudes (e.g., *A. falcatus* and *P. latifolius* in the southern Cape). The distribution of *A. falcatus* in coastal lowland forest at subtropical latitudes of northeastern South Africa and southern Mozambique is unusual and probably relictual, a legacy of former cooler periods during the late Pleistocene and Holocene (Mazus, 2000; Finch and Hill, 2008; Neumann et al., 2008). Confined to the winter rainfall region of the southwestern Cape, *P. elongatus* is unique among African members of the Podocarpaceae in its ability to regenerate from roots (Midgley et al., 1995a).

BIOGEOGRAPHY

The earliest records of African taxa possibly belonging to the Podocarpaceae arise in the Jurassic in Morocco, followed by Egypt in the Eocene and Ethiopia in the Miocene (Dupéron-Laudoueneix and Dupéron, 1995). Miocene pollen records of Podocarpaceae associated with now extinct taxa in the southwestern Cape support the hypothesis of a common Gondwanan flora (Coetzee and Muller, 1984). Consistent with this proposal are the vicariant distributions of *A. mannii* on São Tomé Island (Maley, 1996b) in the Gulf of Guinea and podocarp genera on Madagascar (Schatz, 1996). With five to seven podocarp taxa, Madagascar has been a center of radiation and, given its Gondwanan distribution adjacent to East Africa, also a site of *Afrocarpus* radiation, suggesting podocarps have expanded their distribution from East Africa. Podocarp fossils first appear in East Africa 14 MYA (Bonnefille, 1994) and in West Africa 2.7 MYA (Morley, 2000, 2003, this volume).

The distribution of podocarps on mainland Africa is reasonably well known, and the family has featured prominently in reconstructing paleoenvironments for the last 150,000 years. In general, African podocarps are restricted to highland archipelagos (sensu White, 1981) that

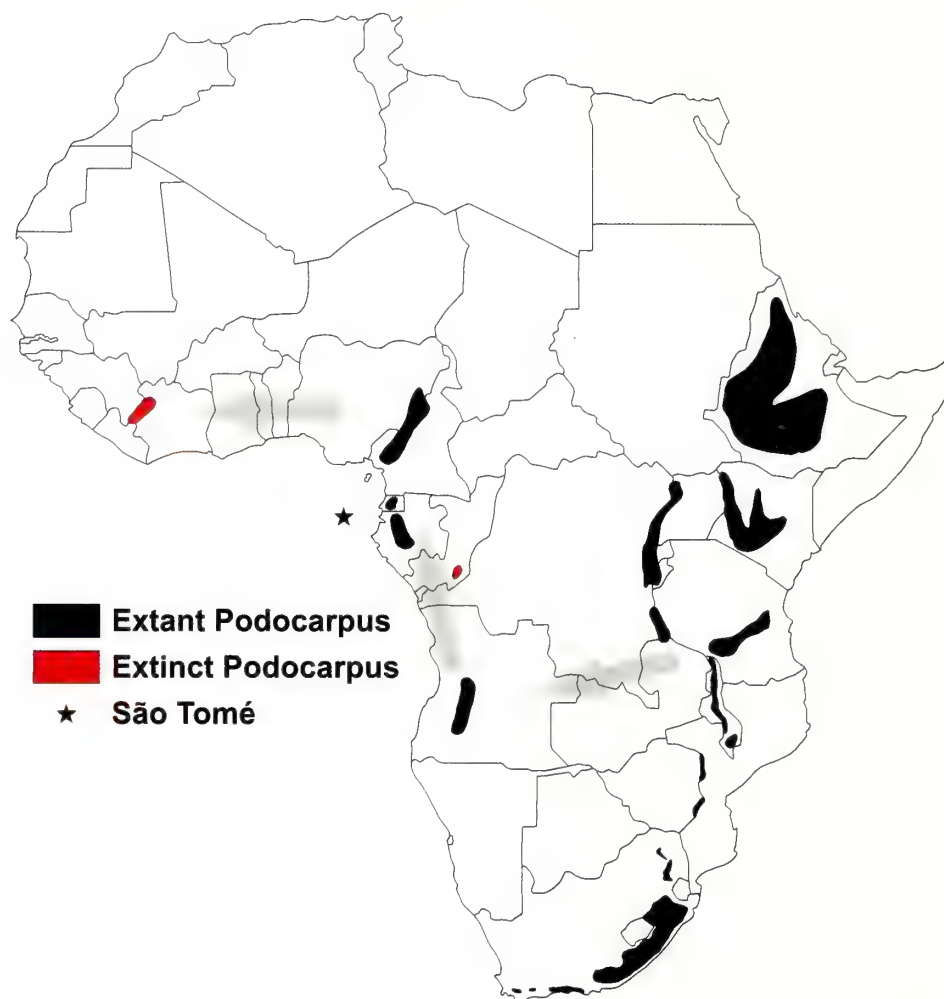


FIGURE 5.1. Highland regions in Africa where Afromontane forest is distributed (adapted from White, 1981). Areas in red indicate now extinct distributions of what is assumed to be *Podocarpus latifolius*. Arrows indicate proposed migration route of Afromontane elements from the East African highland region into West Africa via the Zambezi-Congo watershed (adapted from Maley, 1989). The West African distribution of *P. latifolius* was compiled from multiple sources: western Cameroon highlands (Maley and Brenac, 1998), Equatorial Guinea (Parmentier et al., 2001), the Chaillu massif in Gabon (Maley et al., 1990), west central highlands (Huambe) of Angola (Huntley and Matos, 1994), southeastern Congo highlands (Malaisse, 1967). Pollen cores from multiple marine and terrestrial sites in West Africa attest to a former distribution in the Guinean highlands (Maley, 1993; Dupont et al., 2000) and the Batéké Plateau of Congo (Elenga et al., 1991).

correspond with regions of high species richness and endemism that are considered refuges during extreme paleoclimatic conditions (White, 1981; Maley, 1989; Linder, 2001; Figure 5.1). The principal Afromontane forest belt extends intermittently from Ethiopia southward to the southern Cape. *Afrocarpus* is distributed throughout this region but is absent from West Africa. *Podocarpus* has an isolated distribution in West Africa, extending from the

Cameroon highlands as far south as central Angola, and occurs throughout the East African mountain chain but is absent from Ethiopia. At the landscape scale, Afromontane forests persist as relatively small patches within a grassland or fynbos/heathland matrix (Figure 5.2).

Sharing of Afromontane faunal and floral elements between the Cameroon highlands and East Africa has long been recognized (Moreau, 1966; Kingdon, 1971;

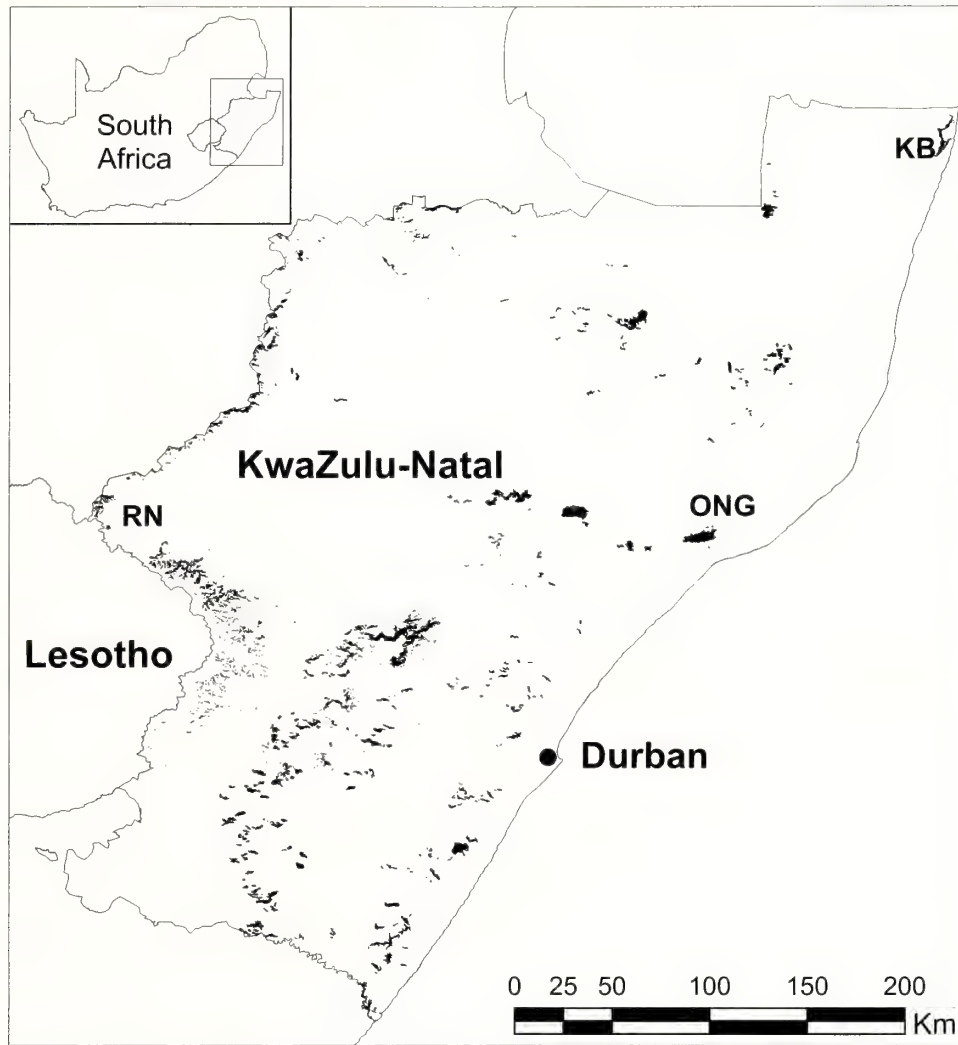


FIGURE 5.2. Indigenous forest in KwaZulu-Natal, South Africa, showing the patchy distribution at the landscape scale. Sites referred to in the text are Royal Natal (RN), Ongoye (ONG), and Kosi Bay (KB).

White, 1978, 1981; Hamilton, 1989; Dawson and Powell, 1999). An explanation for this disjunct distribution is that a direct dispersal corridor opened during drier climatic periods (Moreau, 1966; Van Zinderen Bakker, 1967; Coetsee and Van Zinderen Bakker, 1970; Kingdon, 1971). On the basis of montane floral elements, however, White (1981), and later Maley (1989, 1996a), proposed a more southern migration route that avoided the central Congo basin (Figure 5.1). In support of this pathway, Linder (2001) recently identified the Zambezi–Congo watershed, extending from northern Zambia to central Angola, as an important center of plant species diversity and endemism.

Determining the timing of migration between East and West Africa is difficult given the long history of podocarps in West Africa (2.7 MYA; Morley, 2000, 2003, this volume). Repeated climatic oscillations in the last 800,000 years, and in particular the last 150,000 years, for which the pollen record is well known (Maley, 1993; Dupont et al., 2000), provide adequate opportunity for biotic movement via the proposed Zambezi–Congo watershed corridor to West Africa. The significant increase in montane elements (particularly podocarps) in East Africa from 115,000 to 95,000 years ago reflects the expansion of montane forest taxa to lowland areas associated with cooler and dryer conditions (Cohen et al., 2007). At

much the same time, two phases of cool and dry conditions (115,000–105,000 and 95,000–85,000 years ago) resulted in maximum expansion of montane elements in West Africa (Fredoux, 1994; Maley, 1996a; Dupont et al., 2000). At no stage, even during the Last Glacial Maximum (18,000 years ago), does podocarp pollen dominate the record as much as in that earlier time period.

Even though the taxonomy and systematics of African Podocarpaceae require further refinement, the intriguing differences in distribution between *Podocarpus* and *Afrocarpus* invite speculation. In West Africa, podocarp pollen assumed to be *P. latifolius* was last recorded from the Guinean highlands approximately 74,000 years ago (Fredoux, 1994; Jahns et al., 1998; Dupont et al., 2000) and from the Batéké Plateau in the Congo Republic just prior to the Holocene (Elenga et al., 1991). Apart from the isolated distribution of *A. mannii* on São Tomé Island in the Gulf of Guinea, *Afrocarpus* has not been recorded from West Africa. *Afrocarpus* is the only podocarp in Ethiopia but coexists with *Podocarpus* throughout East and southern Africa. The absence of *Podocarpus* from Ethiopia is unusual since many common Afromontane tree species occur in the region (White, 1978; Dawson and Powell, 1999). Regional extinction is plausible given the history of local extinction of *Podocarpus* (assumed) in West Africa (Elenga et al., 1991; Dupont et al., 2000). The relatively impoverished bird and butterfly faunas of Ethiopia and the high endemism of the latter (Carcasson, 1964; Moreau, 1966) suggest the region has long been isolated, adding support to the extinction hypothesis. However, shared bird subspecies between Ethiopia and Kenya imply a recent biotic exchange (Moreau, 1966), at least for vagile animal species, but does not explain the absence of *P. latifolius*, an otherwise widely distributed podocarp, from Ethiopia.

A consistent pattern from soil cores in Africa is the concomitant increase in podocarp and grass pollen, associated with the regression of rainforest elements (Meadows, 1984; Fredoux, 1994; Dupont et al., 2000; Neumann et al., 2008). Even when an increase in podocarp pollen is associated with a simultaneous decline in grass (e.g., DeBusk, 1998; Cohen et al., 2007), the proportion of grass in the pollen record is still high (20% or more). An abundance of grass in pollen cores is always characteristic of open habitats (Vincens et al., 2006) and is frequently associated with cooler conditions. In East and West Africa, temperature declines of 4°C or more were associated with the expansion of Afromontane elements to lower elevations and the contraction of tropical (lowland) rainforest (Van Zinderen Bakker, 1982; Bonnefille et al., 1990; Maley, 1996a). Given the

abundance of grass during these cooler periods, Afromontane forest is unlikely to have extended its distribution as a continuous belt. Indeed, contemporary Afromontane landscapes are a patchy mosaic of forest and grassland, with forest patches usually situated on south-facing slopes or in valley heads (Everard, 1986; Meadows and Linder, 1993; Adie and Lawes, 2009b; Figure 5.2). Fire in the grassland matrix is the dominant process responsible for this patchy and isolated distribution of forest (Geldenhuys, 1994). The migration of Afrotropical elements during late Pleistocene climatic fluctuations is therefore most likely to have followed the “stepping-stone” process (DeBusk, 1998), which requires dispersal across an inhospitable grassland matrix. This proposal is consistent with the forest-grassland mosaic typical of the Drakensberg Mountains of eastern South Africa, where all forest tree species, and especially *P. latifolius*, persist in fire refugia situated in the grassland matrix (Adie and Lawes, 2009b; Figure 5.3). Being bird dispersed and capable of rapid germination (4–6 weeks, H. Adie and M. J. Lawes, unpublished data; Geldenhuys, 1993) in a variety of habitats, *P. latifolius* displays traits typical of a highly vagile species. *Podocarpus latifolius*, therefore, fits the model of a good disperser with a high probability of establishment within a grass-dominated environment, provided it can escape fire. However, the species appears to be a weak competitor at the regeneration phase when faced with lowland angiosperm species (Adie and Lawes, unpublished), which may account for its failure to persist in isolated refuges once warmer conditions return that favor lowland forest species.

In contrast to *Podocarpus*, the absence of *Afrocarpus* west of the Eastern Afromontane chain suggests this taxon never extended farther westward. We propose that the westward expansion of *Afrocarpus* has been constrained by its reproductive biology. Dispersed by birds, bats, monkeys, and baboons (Geldenhuys, 1993; Teketay and Granstrom, 1997; Negash, 2003; Hitimana et al., 2004), the *falcatus*–*gracilior* group is unlikely to be dispersal limited, even across the open grass-dominated landscapes that characterize the Afrotropical region. However, the hard sclerotesta of *A. falcatus* cones delays germination for a year or more and leads to high postdispersal damage by mammals, resulting in low recruitment rates (Geldenhuys, 1993). In addition, seed viability declines by more than 50% within 12 months of harvesting (Negash, 2003). Loss of viability and postdispersal mortality combined with infrequent seed production (mast fruiter) all reduce the probability of colonizing new habitat. At the landscape scale, *Afrocarpus* appears to be a poor colonist but persists well once established. The minor radiation



FIGURE 5.3. Mature *Podocarpus latifolius* persisting in a fire-safe topographic refuge situated in a regularly burnt grassland matrix at Royal Natal.

of *Afrocarpus* in East Africa and the discovery of distinct *A. falcatus* provenances in South Africa (Geldenhuys and Von dem Bussche, 1997) are consistent with the hypothesis that the genus is restricted by stepping-stone dispersal and imply that the distribution of *Afrocarpus* in Africa is an ancient one.

PODOCARP ECOPHYSIOLOGY

The ecophysiology of African podocarps is largely unknown. Nevertheless, explanations for conifer distribution in Africa have been based in large part on physiological differences between conifers and competing angiosperms

(Bond, 1989). Bond argued that functional constraints such as tracheids and nonvascularized leaves place conifers at a competitive disadvantage at the regeneration phase, restricting them to edaphically or climatically sub-optimal sites where they perform better than angiosperms.

The dual role of mechanical support and hydraulic function performed by wood leads to trade-offs in performance with important ecological implications (Chave et al., 2009). Angiosperms solved this problem by separating mechanical support from hydraulic function with the evolution of xylem vessels, multicellular conduits for water transport, and a matrix of fibers for support (Sperry et al., 2006). Released from their structural function, angiosperm vessels achieve greater conducting efficiency by increasing

their diameter (Tyree and Ewers, 1991; Sperry et al., 2005). In contrast, conifer tracheids are limited by their unicellularity and the need to provide both mechanical support and hydraulic function to the plant (Sperry et al., 2006; Lusk, this volume; Brodribb, this volume). The dual role of tracheids leads to a trade-off between their two primary functions, a constraint that conifers have overcome to some extent with the evolution of the torus-margo pit, a membrane that joins conduit end-walls, allowing significantly higher conductivity compared with the longer vessels of angiosperms (Hacke et al., 2004; Pittermann et al., 2005). Nevertheless, conifers grow more slowly than angiosperms (Coomes and Bellingham, this volume).

Compared to angiosperms, conifer leaves are poorly vascularized and have low stomatal conductance and low specific leaf area, resulting in lower photosynthetic capacity (Lusk et al., 2003; Brodribb et al., 2005a, 2005b). Photosynthetic capacity increases with xylem vessel conductance (Brodribb and Feild, 2000; Hubbard et al., 2001), but large vessels are at risk of embolism in cold environments (Sperry et al., 1994). Photosynthetic yield (measured by the leaf area to stem area ratio) has been shown to be much greater in angiosperms measured in high light, but this advantage over conifers tends to be neutralized in low light (Brodribb et al., 2005a). A pervasive pattern among African podocarps is superior shade tolerance compared with associated angiosperms, which demand more light (Midgley et al., 1995b; Adie and Lawes, 2009a). However, Coomes and Bellingham (this volume) point out that many shade-tolerant podocarps are capable of regenerating in shaded environments yet fail in deep shade, where light levels are ~2% of daylight. This is consistent with the finding that plants, in general, are substantially more responsive to nutrient supply at light levels of >5% of daylight compared with deep understory shade, where light levels are often <2% of daylight (Coomes and Grubb, 2000). Thus, it is not surprising that relative shade tolerance of podocarps is strongly implicated in the coexistence of African podocarps and angiosperms and is likely the dominant determinant of mixed angiosperm–conifer tree community structure in African forests (Adie and Lawes, 2009a).

ECOLOGY

MIXED ANGIOSPERM–CONIFER FORESTS

Here we examine podocarp regeneration along an altitudinal gradient extending from the Drakensberg,

a mountainous region situated in the northwest of KwaZulu-Natal province, to lowland forest on the east coast of South Africa (Figure 5.2). Mixed angiosperm–conifer forests in the montane region are characteristically small, usually less than 5 ha and rarely exceeding 30 ha (Lawes et al., 2007a), and exist as an archipelago within a grassland matrix between 1,400 and 1,830 m above sea level. Forest distribution is limited by fire and is therefore generally restricted to moist south-facing slopes and steep-sided ravines (Everard, 1986; Geldenhuys, 1994) situated beneath tall sandstone cliffs. Lowland forest lies on the plains inland of the coastal dune cordon (Mucina and Rutherford, 2006) and is well represented just south of Kosi Bay in northern Maputaland (Figure 5.2). The forests have a well-developed canopy and subcanopy, and the semiwoody herb *Isoglossa woodii* (Acanthaceae) frequently dominates the shrub layer. Intermediate between the inland mountains and coastal lowlands is coastal scarp forest, a species-rich subtropical forest type that is derived from, and hence owes its diversity to, tropical coastal forests and inland Afromontane elements (Lawes, 1990; Griffiths and Lawes, 2006). Situated in a mosaic of grasslands and rocky granitic outcrops, Ongoye Forest Reserve lies between 300 and 500 m elevation and is 2,600 ha in extent (Boudreau et al., 2005).

Three species of Podocarpaceae are distributed along the described altitudinal gradient. *Podocarpus latifolius* is an abundant and widespread species throughout the Drakensberg and KwaZulu-Natal midlands and extends toward the coast, where it is an uncommon component of scarp forest. Known from only one forest in the Drakensberg, *P. henkelii* is rare in the montane region but common in mist belt forests of the midlands (H. Adie, personal observation). *Afrocarpus falcatus* has a patchy but locally common distribution in the Drakensberg, is widespread and relatively common in the midlands, is present but uncommon in scarp forest, and is the only podocarp found in the subtropical lowland forests of the coastal plains, where it is scarce.

BIOPHYSICAL FACTORS

Light is a critical factor determining plant growth and survival in forest ecosystems (Denslow, 1987), in which the differential response to light during the regeneration phase drives plant community composition and dynamics (Kobe et al., 1995; Bloor and Grubb, 2003). In mixed angiosperm–conifer forests of the Southern Hemisphere, regeneration following both autogenic and allogenic disturbance is driven by differences in plant shade tolerance

(Lusk and Ogden, 1992; Ogden and Stewart, 1995; Lusk and Smith, 1998). Deep shade (~2% daylight) in southern forests tends to favor angiosperms at the expense of podocarps (Lusk, 1996; Coomes et al., 2005).

To understand regeneration patterns in Afromontane forest, two forest types that differed substantially in structure and, therefore, in light environment were compared. Angiosperm forest, as the name implies, is dominated by angiosperm canopy species. Tree density in this forest type is relatively high, and the forest canopy is moderate in stature (<20 m). *Podocarpus latifolius* is usually present in the angiosperm forest canopy, but at low density. Forests dominated by the conifer (>60% of canopy trees) differ structurally from those dominated by angiosperms by having a higher canopy (20–25 m) and larger trees with greater nearest neighbor distances, resulting in an open mid-story and “cathedral-like” structure. The two forest types differ in terms of the quality and quantity of light

reaching the forest floor beneath the intact canopy and in canopy gaps (Adie and Lawes, 2009a; Figure 5.4). Photosynthetically active radiation was high (~17% irradiance) in canopy gaps in both forest types, but light quality (measured as the ratio of red to far red light; Capers and Chazdon, 2004) in angiosperm canopy gaps, which were small ($84.6 \pm 13.7 \text{ m}^2$, $n = 10$), showed far less variation and was lower compared with the much larger gaps ($183 \text{ m}^2 \pm 36.6$, $n = 10$) in *Podocarpus* forest (Adie and Lawes, 2009a). We also sampled forest tree regeneration outside true forest, in a thicket environment dominated by *Rhus tomentosa*. The thicket habitat, which had a low canopy of 4–6 m, was less shaded than the two forest habitats, but light quality was substantially lower, probably because of the high stem density of the habitat (Lee, 1989; Smith and Whitlam, 1997).

The structural conditions described above cause important differences in the light reaching the forest

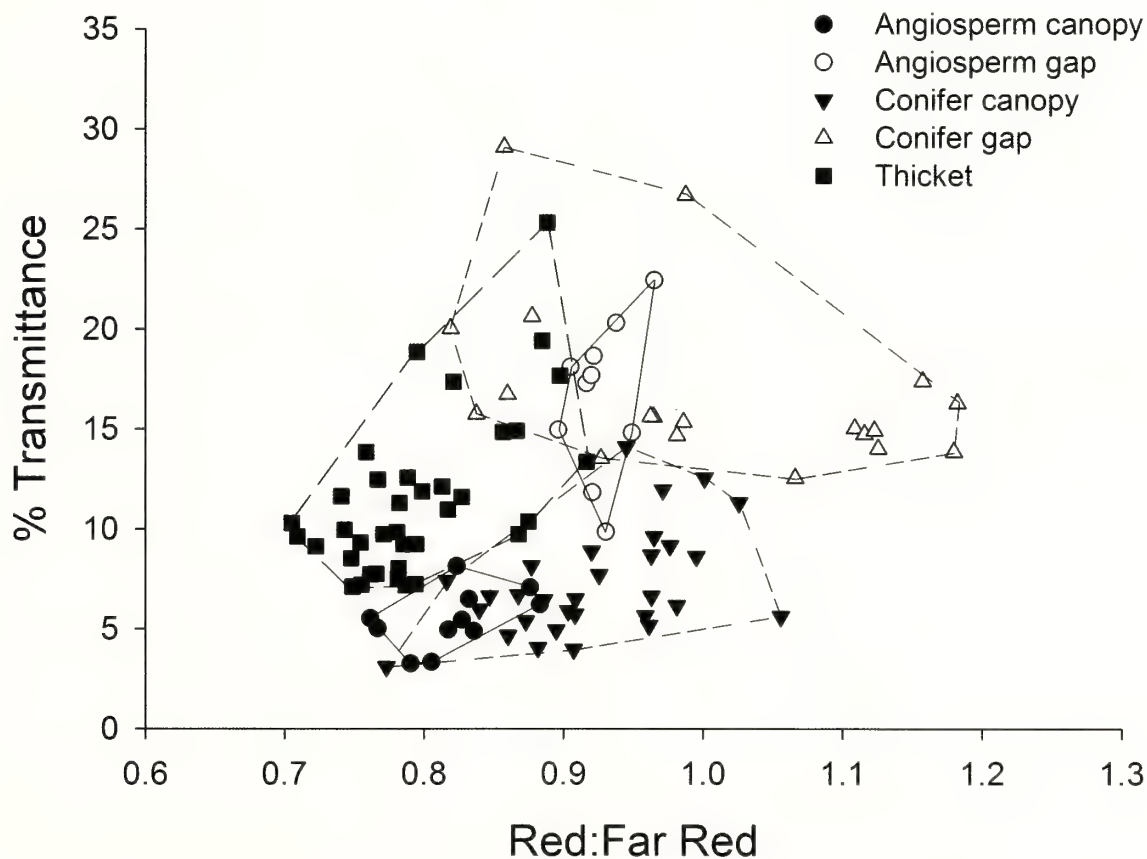


FIGURE 5.4. Light characteristics (percent light transmittance, red:far red) at ground level in *Rhus tomentosa* thicket and two habitats (canopy, gap) in forest dominated by angiosperms and conifers.

understory environment, and both light and the understory vegetation act in combination to restrict regeneration by forest canopy species (Adie and Lawes, 2009a). Grass was the principal ground cover beneath the intact *Podocarpus* forest canopy, but was absent from both angiosperm forest and thicket. Bare ground or a sparse covering of litter dominated the thicket habitat and angiosperm forest. Gaps in both forest types were frequently choked by a combination of grasses, vines, ferns, and understory shrubs. With this background to the physical environment, we discuss the relative success of angiosperm and conifer regeneration in Afrotropical forest.

THE ROLE OF DISTURBANCE IN MIXED ANGIOSPERM-CONIFER FORESTS IN SOUTH AFRICA

GAP-PHASE DYNAMICS

Gap-phase dynamics is an important driver of forest structure and dynamics in New Zealand and South America (Lusk and Ogden, 1992; Ogden and Stewart, 1995). In these temperate forests, the differential response to gaps at the juvenile stage leads to canopy species coexistence (Lusk and Smith, 1998; Gutierrez et al., 2004; Gutierrez et al., 2008). In contrast, canopy gaps have a limited role in the regeneration dynamics of Afrotropical forests (Adie and Lawes, 2009b), where poor regeneration by angiosperm canopy species results from their shade intolerance (Midgley et al., 1995b; Adie and Lawes, 2009a).

Gaps in angiosperm forest are created by lateral branch breakage and stem snapping, resulting in relatively small gaps. Young gaps tend to be larger than old gaps, suggestive of progressive canopy closure with age due to lateral ingrowth of adjacent canopies. Interestingly, seedling and sapling densities do not differ among gap sizes or from densities recorded beneath the closed canopy (Adie and Lawes, 2009a). Thus, in spite of elevated light levels, the gap environment offers no new regeneration opportunities for angiosperms or *P. latifolius*. Even though angiosperm seedlings were abundant, very few saplings or poles were recorded in gaps or beneath the canopy (Figure 5.5), suggesting that light conditions were inadequate for growth into larger size categories. Young conifer trees were abundant in these regeneration environments, but less so in older gaps, implying self-thinning or suppression by ground cover (Beckage et al., 2000; Coomes et al., 2005). In addition, *P. latifolius* saplings (1–5 cm diameter at breast height [dbh]) and poles (5 cm < dbh ≤ 10 cm)

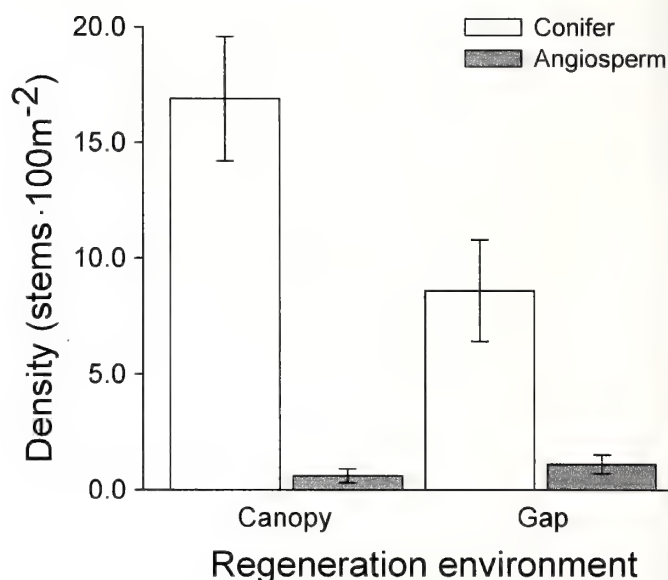


FIGURE 5.5. Mean density (\pm standard error, $n = 10$) of young conifer and angiosperm trees in two regeneration environments in Afrotropical forest.

were common in young tree fall gaps (<24 months old), demonstrating that successful gap fillers were drawn from individuals in the advanced regeneration phase that established prior to gap creation (Adie and Lawes, 2009b). Being shade tolerant, or more shade tolerant than associated angiosperm species, the conifer outperformed angiosperms at gap formation because it was able to establish profusely beneath the angiosperm canopy.

In contrast to the high rate of establishment by *P. latifolius* in angiosperm forest, regeneration by the conifer in *Podocarpus*-dominated forest was substantially less than that recorded for angiosperms (Adie and Lawes, 2009a). Canopy gaps in *Podocarpus* forest were generally created by uprooting of large-canopy individuals (Adie and Lawes, 2009b). Consequently, canopy gaps in *Podocarpus* forest were relatively large compared with angiosperm forest, yet they offered no new regeneration opportunities to angiosperms or *P. latifolius*. Curiously, unlike angiosperm forest, there were almost no *P. latifolius* seedlings beneath the intact canopy of *Podocarpus* forest. Grass, the dominant ground cover in *Podocarpus* forest, suppressed *P. latifolius* seedlings, causing high mortality (Adie and Lawes, 2009b). Even in gaps, the abundant grass cover resulted in relatively low densities of *P. latifolius* (0.9 ± 0.3 per 0.01 ha) and angiosperm canopy species (1.2 ± 0.3 per 0.01 ha).

Besides grass, dense understory vegetation and vines may also dominate gaps. An inverse J-shaped distribution of angiosperm stem sizes in *Podocarpus* forest suggests that grass does not suppress angiosperm seedlings in the same way it does *P. latifolius*. Seedlings were common, but the scarcity of saplings implies growth suppression, with possibly light limitation restricting the growth of seedlings into larger size categories. Notwithstanding the low density of both angiosperms and *P. latifolius* in gaps, the contest between these two plant groups in *Podocarpus* forest is equivocal, with both apparently having an equal opportunity to occupy gaps. Tree fall gaps therefore offer one mechanism to maintain angiosperm diversity in Afrotropical forest, but in old-growth forest only (Adie and Lawes, 2009a).

CATASTROPHIC DISTURBANCE

Large-scale natural disturbances (earthquakes, cyclones, landslides, volcanic eruptions) have had a pervasive influence on the structure and dynamics of mixed angiosperm–conifer forests in New Zealand (Stewart and Rose, 1989; Ogden and Stewart, 1995; Wells et al., 2001) and South America (Veblen and Ashton, 1978; Veblen et al., 1995). The Afrotropical landscape in the subtropics is relatively benign in that it lacks the climatic, topographic, or geological extremes that cause stand-destroying disturbance in many southern temperate forest environments. Fire has also been reported as an important process controlling stand structure in mixed forests in South America (Burns, 1993), and extensive precolonization fires in New Zealand probably caused a mosaic of seral and mature forest communities (Ogden et al., 1998). Natural fire is also implicated in the total destruction of podocarp forests following drought on New Zealand's South Island (Kershaw and McGlone, 1995) and in New Guinea *Araucaria* forest (Enright, 1995). In tropical environments, fires are more likely during drought years, when fragmented forests are particularly vulnerable (Cochrane and Laurance, 2002). South American gallery forest, a naturally fragmented form of tropical moist forest that exists within a savanna matrix (Kellman and Meave, 1997), is more prone to fire in the late dry season, when plant material is more ignitable (Biddulph and Kellman, 1998). Drakensberg montane forest is not unlike gallery forest in that it exists as small patches within a fire-prone grassland matrix (Everard, 1986), yet fire has largely been de-emphasized as a process driving forest change in South Africa (Mucina and Rutherford, 2006), a viewpoint that is not unexpected since fire is unusual in South African forests (Midgley et al., 1997).

Forests with a canopy dominated by angiosperms do not burn (Bond, 1997) because of low fuel loads and high leaf moisture levels (van Wilgen et al., 1990) or high fuel moisture content (Eriksson et al., 2003). Nevertheless, it is notable that most Afrotropical forests establish and persist in fire refugia, where they escape the prevailing grassland fire direction (Geldenhuys, 1994).

Although rare under the present grassland management system in the subtropics of southern Africa, fire may have been a critical historical driver of inland forest structure and dynamics by destroying old-growth *Podocarpus* forest. Catastrophic disturbance provides relatively rare regeneration opportunities for angiosperm trees in the Afrotropical landscape. Historical records report catastrophic fires devastating indigenous forest, particularly in the temperate *Podocarpus* forests of the southern Cape (Geldenhuys, 1994). In most cases fires were preceded by several days of hot berg wind conditions (van Wilgen, 1984; Geldenhuys, 1994; Bond, 1997). The open physiognomy of *Podocarpus*-dominated forests is highly susceptible to the desiccating effect of berg winds and, coupled with high levels of volatile compounds in long-lived sclerophyllous leaves (Kershaw and McGlone, 1995) and the well-developed grass cover in old-growth forests, predisposes *Podocarpus* forest to fire.

DOES PATTERN AND PROCESS IN AFROMONTANE FORESTS CONFORM TO OTHER SOUTHERN HEMISPHERE PODOCARP FORESTS?

Regeneration patterns of canopy trees in montane forests are consistent with the temporal stand replacement model (TSRM; Ogden, 1985; Enright et al., 1999; Ogden et al., 2005), with important exceptions. The TSRM was proposed to explain the dominance of long-lived pioneer conifer cohorts and the widespread regeneration failure reported from temperate forests in New Zealand (Veblen and Stewart, 1982; Stewart and Rose, 1989) and South America (Veblen et al., 1980, 1995). Under the TSRM, sites are colonized by a pioneer cohort, usually a long-lived conifer, following stand-destroying disturbance. In the absence of further disturbance, synchronous senescence by the colonizing cohort causes overstory mortality, creating gaps that offer diminishing regeneration opportunities for the first-generation conifer in favor of more shade-tolerant species, usually an angiosperm (Enright et al., 1999; Ogden et al., 2005).

Regeneration failure by the angiosperm canopy component is a recurrent pattern in South African inland forests

(Moll, 1972; Everard et al., 1995; West et al., 2000; Lawes et al., 2007b). Drakensberg montane forests, with a near absence of advanced angiosperm regeneration beneath the intact canopy, are no exception (Adie and Lawes, 2009b). However, angiosperm regeneration was recorded from scrub thicket sites and a grassland fire-exclusion site, leading us to propose that many angiosperm species assume a colonizing role and establish as a pioneer cohort following disturbance (Adie and Lawes, 2009b). Unlike temperate forests elsewhere, *P. latifolius* was slow to regenerate in these scrub environments, possibly because of slow seedling growth rates relative to angiosperms (Bond, 1989). The prevalence of angiosperm-dominated canopies among forests that were logged extensively (i.e., catastrophic disturbance) during the colonial era from the early to mid-1800s to the early twentieth century (Fourcade, 1889; Hutchins, 1905; McCracken, 1986) is consistent with the proposal that angiosperms assume the colonizing role following major disturbance. Therefore, in South Africa a suite of angiosperm species take on the pioneer role that is usually filled by a long-lived gymnosperm species in New Zealand. The slow colonization of fire-protected grassland sites by angiosperm tree species demonstrates that catastrophic disturbance, another key feature of the TSRM, is not a necessary requirement for forest development in the Afrotropical landscape.

Podocarpus latifolius regenerated continuously beneath the intact angiosperm-dominated canopy in the Drakensberg, confirming shade tolerance in this species. Age data for *P. latifolius*, which shows that *Podocarpus*-dominated forest is considerably older than angiosperm forest, confirms the replacement of angiosperms by the conifer and is consistent with the TSRM as a two-phase system with phases separated in time (Adie and Lawes, 2009b). Continuous regeneration by the shade-tolerant conifer eliminates the need for the synchronous canopy senescence that is a key feature of the TSRM in other southern temperate forests. Conifer persistence, the central feature of conifer-angiosperm competition, appears to be curtailed by more shade-tolerant angiosperms elsewhere. Superior angiosperm shade tolerance in Chilean temperate forest prevents conifer regeneration in deep shade (Lusk, 1996), and productive alluvial forest habitats in New Zealand appear too dark for even the most shade-tolerant conifers (Coomes et al., 2005). Indeed, the progressive replacement of the colonizing cohort by more shade-tolerant angiosperm species in southern temperate forest is a key feature of the TSRM (Enright and Ogden, 1995; Ogden et al., 2005). In these temperate forests, canopy gaps favor recruitment by conifers, leading to their coexistence with

angiosperms (Lusk and Smith, 1998). The differential response by tree species to varying light conditions is a critical driver of forest structure and dynamics in New Zealand (Ogden and Stewart, 1995). More recently, soil nutrient availability has been shown to have an important role in plant community development, with conifers performing better than angiosperms on nutrient-poor sites (Richardson et al., 2004; Coomes et al., 2005; Carswell et al., 2007).

SOIL NUTRIENTS

Superior shade tolerance of *P. latifolius* in the Afrotropical environment relative to angiosperms weakens the proposition that conifers are restricted to suboptimal environments (climate, nutrients) by competitively superior angiosperms at the regeneration phase (Bond, 1989). Angiosperm shade intolerance removes competition at the conifer seedling phase and ultimately results in the replacement of angiosperms by the podocarp. Do depleted soil nutrient levels affect the tortoise-hare contest in favor of the conifer as Bond (1989) predicted? In New Zealand, soil nutrient status alters regeneration success among podocarps (Carswell et al., 2007), and podocarps perform better on infertile (phosphorus-limited) and poorly drained soils relative to co-occurring angiosperms (Richardson et al., 2004; Coomes et al., 2005). The role of soil fertility in altering the outcome of the angiosperm-podocarp contest has not been examined directly in African forests. At fynbos sites, known to be very infertile, shaded microhabitats were more important than soil organic matter content for germination of forest species (Cowling et al., 1997), and in the southern Cape, topography and aspect, rather than soil type, determined forest distribution (Geldenhuys, 1994). In these regions fire was the overriding process determining forest distribution (van Wilgen et al., 1990; Geldenhuys, 1994; Cowling et al., 1997).

Compared with *P. latifolius*, which showed no nutrient effect, seedling growth of angiosperm canopy species was consistently higher at high nitrogen (half-strength Hoagland's solution containing 10% of the recommended nitrogen concentration; Hewitt, 1966) compared with low nitrogen (1% nitrogen) levels, but there was a steady decline in performance with diminishing light (Figure 5.6). In Chilean temperate rainforest, shade-tolerant conifers were associated with nutrient-poor and climatically stressed sites, but these species were also associated with high-disturbance gap sites (Lusk, 1996), suggesting response to light is equally, if not more, important to regeneration success. Coomes et al. (2005) showed variable performance by conifers along a productivity gradient,

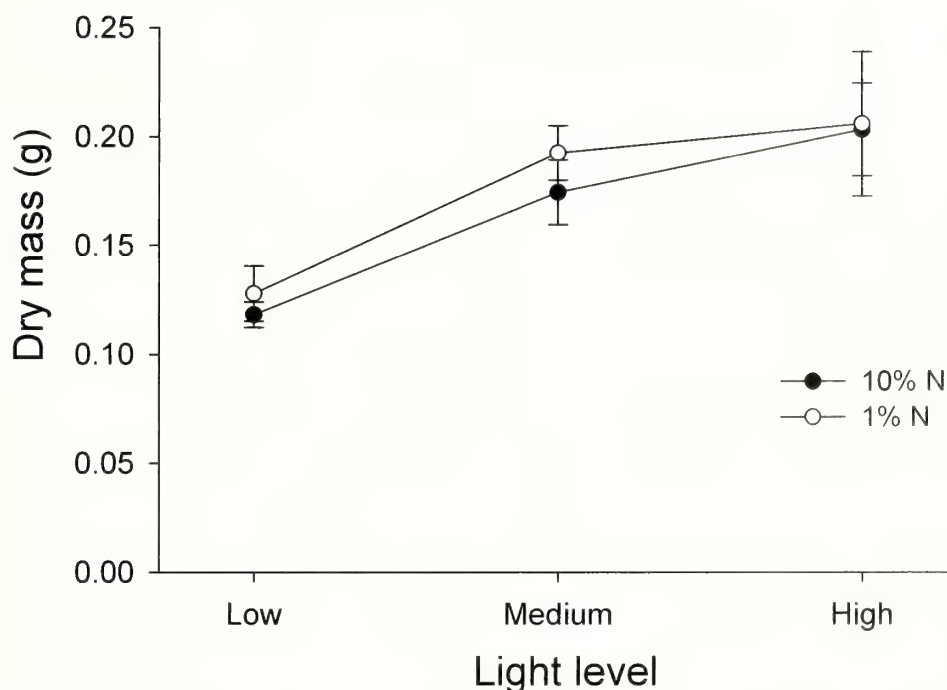


FIGURE 5.6. Seedling mass (mean \pm standard error, $n = 6$) of *P. latifolius* after three months growth under three light treatments (low = 2.4% photosynthetically active radiation (PAR), medium = 8.0% PAR, and high = 13.5% PAR) and two nutrient levels (10% nitrogen and 1% nitrogen).

the conifers performing better in lower-nutrient (yet more open) terrace forest, where they established in gaps. In contrast, shadier habitats and ferns limited regeneration opportunities for conifers at the upper end of the productivity gradient. In Afromontane forests of the South African Drakensberg Mountains we found no association between conifer or angiosperm community dominance and soil chemical composition (M. J. Lawes, unpublished data). Nitrogen does not appear to be a limiting soil nutrient in African forest sites. In the Munesa region of the Ethiopian southeastern highlands, where *A. falcatus* is an important canopy species, the soil carbon to nitrogen ratio was 12.6 (Solomon et al., 2002). This value is no different from values for Drakensberg and subtropical forest sites in KwaZulu-Natal (Table 5.2) but is substantially lower than nutrient-poor sites in New Zealand (Richardson et al., 2004; Coomes et al., 2005). We have no comparable values for total phosphorus, which has been shown to be a strong driver of plant community structure in New Zealand forests (Richardson et al., 2004; Coomes et al., 2005; Carswell et al., 2007). However, available phosphorus, the quantity of phosphorus that is easily extracted and directly available to the plant (Holford, 1997), does not seem to

be limiting in the Drakensberg or subtropical scarp forest sites (Table 5.2). Concentrations of available phosphorus $>10 \text{ mg kg}^{-1}$ (Ambic-2 method; Thibaud et al., 1994) in similar soils are not considered severely limiting for annual agricultural crops in KwaZulu-Natal; it is therefore unlikely that concentrations $>5 \text{ mg kg}^{-1}$ would be limiting for slow-growing forest trees (A. Manson, Soil Fertility Analytical Services, KZN Department of Agriculture and Environmental Affairs, personal communication). Available phosphorus recorded in forests in the central Ethiopian highlands (31.7 mg kg^{-1} ; Bray II method; Michelsen et al., 1996) was similar to Ongoye forest. These data indicate that soils in southeastern Africa are neither nitrogen nor phosphorus limited, and it is possible that soil moisture may have an importance not recognized in other Southern Hemisphere locations where podocarps are present.

Arbuscular mycorrhizal fungi provide an important mechanism to overcome growth constraints imposed by nutrient-poor soils (Brundrett, 2002). Such fungi have a significant effect on seedling growth (Janos, 1980), particularly in soils where available phosphorus concentrations are low (Chen et al., 2005; Lambers et al., 2008), and have the potential of causing differential regeneration success

TABLE 5.2. Soil chemical characteristics (mean \pm standard error, $n = 6$) from forest sites in the Drakensberg (Monk's Cowl, Royal Natal) and a subtropical site (Ongoye Forest Reserve) in KwaZulu-Natal. Available phosphorus was analyzed using the Ambic-2 method (Thibaud et al., 1994).

Site	C:N	Total N (%)	Available P (mg P kg ⁻¹)
Royal Natal	12.06 \pm 0.81	0.91 \pm 0.045	12.89 \pm 0.876
Monk's Cowl	12.55 \pm 0.62	1.21 \pm 0.171	9.88 \pm 1.04
Ongoye	11.77 \pm 0.60	0.71 \pm 0.215	27.68 \pm 1.42

and therefore affecting species diversity in forests (Kiers et al., 2000; Chen et al., 2005). Phosphorus uptake by conifer roots is stimulated by the presence of arbuscular mycorrhizal fungi (Morrison and English, 1967; Baylis, 1969), and Dickie and Holdaway (this volume) propose that root nodules serve to increase the volume of the root cortex volume, resulting in greater fungal infection. Arbuscular mycorrhizas have been identified in *A. falcatus* (Allsopp and Stock, 1993; Wubet et al., 2003) and *P. latifolius* (Hawley and Dames, 2004) and are also present in many associated angiosperm species in Afrotropical forest (Hawley and Dames, 2004). The importance of arbuscular mycorrhizal fungi at the regeneration phase, and whether it affects the conifer–angiosperm contest, is unknown for Afrotropical forests but is unlikely if phosphorus is not limiting.

PODOCARPS IN COASTAL FOREST

The presence of podocarps in coastal forest is probably a legacy of climatic extremes during the Last Glacial Maximum, when inland forests are thought to have retreated toward the coast (Eeley et al., 1999). *Podocarpus latifolius* persists as large-canopy individuals in scarp forest, but the continuous regeneration so prevalent in montane forest is absent. Seedlings and saplings beneath the canopy are rare and tend to be spindly in appearance (Adie and Lawes, unpublished data). However, angiosperm species are similarly absent from the understory at Ongoye, which contradicts the view that direct competitive interactions limit the conifer beneath the forest canopy in subtropical environments (Midgley et al., 1995a). Either (1) shade tolerance of *P. latifolius* in scarp forest differs from that in montane forest populations, which is not an unreasonable hypothesis since there is evidence for distinct *A. falcatus*

provenances in southern Africa (Geldenhuys and Von dem Bussche, 1997), or (2) the response to light by *P. latifolius* does not differ between the two forest habitats, but there is a lower limit below which the conifer is unable to perform. Incoming photosynthetically active radiation beneath the intact canopy at Ongoye was substantially lower than that recorded in Afrotropical forests (Figure 5.7) because of a more-productive angiosperm canopy and many shade-tolerant mid-canopy species in scarp forest. Deep shade (<2% photosynthetically active radiation) and not direct competition from understory angiosperms, which were absent beneath the canopy, seems to be a more likely mechanism suppressing *P. latifolius* regeneration in scarp forest. Many podocarp species persist in deep shade but do not regenerate continuously in these habitats (Coomes and Bellingham, this volume).

Conifer regeneration opportunities were similarly restricted in productive alluvial forest habitats in New Zealand (Coomes et al., 2005). Saplings of *P. latifolius* growing adjacent to forest roads and on the forest edge at Ongoye were robust (Adie and Lawes, unpublished data), reflecting successful growth and supporting our contention that light, rather than direct angiosperm competition at the regeneration phase, ultimately suppresses growth of this species in scarp forest. Enhanced productivity in scarp forest, which may result from a combination of soil fertility and climate, is a proximate factor that operates indirectly by altering light levels that suppress *P. latifolius* performance.

The differential response to light between angiosperms and conifers appears to be the critical factor driving lowland forest dynamics. An isolated population of *A. falcatus* exists in tropical coastal lowland forest at Kosi Bay in northern Maputaland (Figure 5.2). *Afrocarpus falcatus* is a shade-tolerant tree (Fetene and Feleke, 2001; Tesfaye et al., 2002) that regenerates continuously in forest but has higher seedling growth rates in gaps compared with more shaded sites (Teketay, 1997). The latter point concurs with the observation of Laughton (1938), who considered *A. falcatus* more light demanding than *P. latifolius* in southern Cape forests.

At Kosi Bay the structure of the *A. falcatus* population is consistent with regeneration failure. Very large canopy individuals (>60 cm diameter at breast height) form an integral part of the angiosperm-dominated canopy, with a preponderance of young plants (including seedlings but few saplings) beneath the canopy (R. Kyle, personal communication). Intermediate-sized trees are rare or absent. Saplings and poles are a valuable resource to local communities because the wood is hard and the poles are

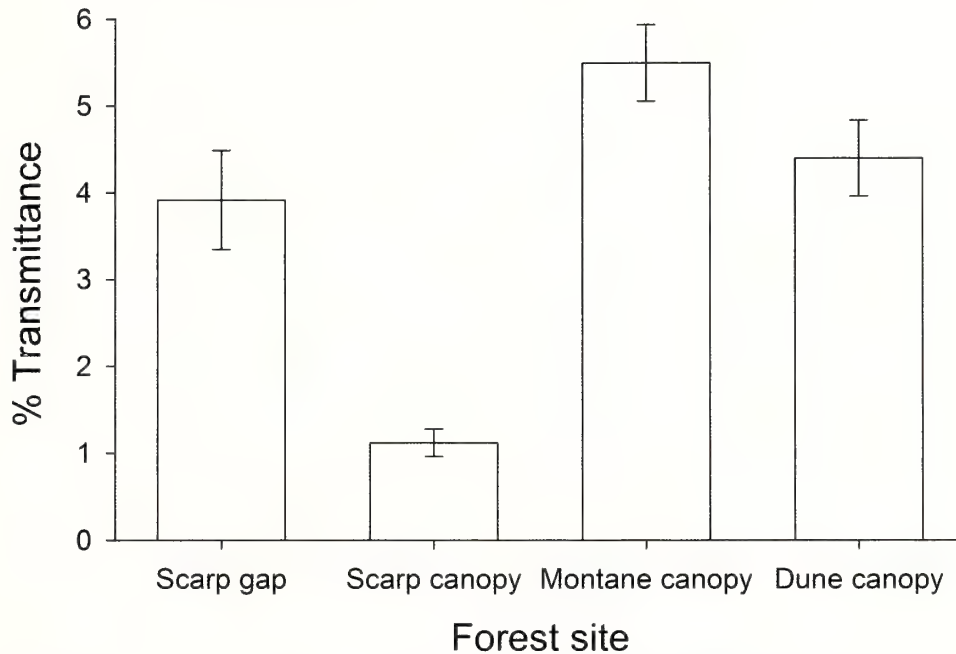


FIGURE 5.7. Mean light transmittance (\pm standard error, $n = 12$) in a scarp forest understory gap and beneath the canopy of scarp forest and angiosperm-dominated Afromontane forest. The gap in scarp forest was created artificially by felling eight mid-canopy tree species.

straight. Consequently, there is heavy harvesting pressure on juvenile plants, which presumably accounts for the paucity of medium-sized trees. Kyle (personal communication) reports that fruiting trees produce abundant fruit and that the high number of seedlings noted in the forest reflects good germination.

Were it not for the intense harvesting pressure on juvenile stages, we suggest that *A. falcatus* would show continuous regeneration in coastal forests. Their establishment beneath the canopy and the straight nature of poles is consistent with shade tolerance for this conifer. It is not clear whether the persistence of *A. falcatus* in subtropical lowland forest is directly associated with its ability to establish in shade or whether there is an interactive effect with soil nutrient status. Coastal forests are dominated by light-demanding angiosperms, with few species showing successful establishment beneath the shaded closed canopy and pervasive shrub layer (Griffiths et al., 2007). The understory herbaceous shrub *Isoglossa woodii* influences forest dynamics by suppressing tree recruitment in dune forest (Griffiths et al., 2007; Tsvuura et al., 2007). The proposition that *A. falcatus* persists in subtropical lowland forest through shade tolerance mirrors our finding for *P. latifolius* in Afromontane forest. However, some

podocarp species are able to persist in lowland tropical forest where soil conditions are poor (Coomes and Bellingham, this volume). Soils in the Kosi Bay system are sandy and infertile (Maud, 1980) and may favor *A. falcatus* over competing angiosperms given the superior ability of conifers to acquire and retain nutrients (Coomes and Bellingham, this volume).

The persistence of *A. falcatus* in coastal lowland habitats is an enigma. Several aspects of the biology of this species would seem to conspire against long-term success. First, regeneration failure is not uncommon among mast-fruited species (Blundell and Peart, 2004), and logging has been shown to reduce the extent and intensity of mast-fruited events, resulting in regeneration failure (Curran et al., 1999). Second, the threat of extinction among dioecious plants, particularly woody species, is high (Vamosi and Vamosi, 2005). Reduced mate assurance leads to pollination failure (Pannell and Barrett, 1998), or reduced seed production limits the effective size of the breeding population (Heilbuth et al., 2001). Third, recruitment rates are generally low because of delayed germination and high postdispersal damage by mammals (Geldenhuys, 1993) and loss of seed viability (Negash, 2003). Finally, sustained harvesting of *A. falcatus* poles has a significant

impact on regeneration success (Tesfaye et al., 2002; Lawes et al., 2007b). The ability to regenerate in shaded environments, compared with an angiosperm component dominated almost entirely by light-demanding species, explains this species' persistence in lowland coastal forest.

CYCLICAL REGENERATION AND PODOCARP PERSISTENCE

The TSRM promotes a deterministic successional process that relies on catastrophic disturbance to initiate the sequence (Ogden, 1985; Ogden and Stewart, 1995). However, catastrophic disturbance is not always necessary to explain forest structure and the persistence of podocarps (Six Dijkstra et al., 1985; Lusk and Ogden, 1992). Podocarps are able to maintain their dominance, or coexistence with angiosperms, through cyclical regeneration driven principally by endogenous disturbance and the differential response of trees at the juvenile stage to canopy opening (Lusk and Smith, 1998). At the landscape scale, tree species coexistence is mediated through temporal (progressive overstory collapse) and spatial (microsite, degree of canopy closure) segregation (Ogden and Stewart, 1995). The duration of the proposed regeneration cycle may last 650–700 years (Beveridge, 1973; Six Dijkstra et al., 1985). In South African Afromontane forests, it is not clear what follows the old-growth *Podocarpus*-dominated phase since not only is this type of forest rare, but these old-growth forests appear to be relatively young. Trees exceeding 600 years in age are routinely recorded from southern temperate forests in New Zealand and Chile (e.g., Lusk and Ogden, 1992; Lusk, 1996; Smale et al., 1997), yet we dated the largest *P. latifolius* to a little over half that age (Adie and Lawes, 2009b).

Several lines of evidence lead to a model that proposes the persistence of old-growth *Podocarpus* forest in the absence of stand-destroying disturbance in South Africa. First, grass suppresses the establishment of *P. latifolius*, restricting regeneration to occasional episodes that may be associated with higher than usual rainfall (Adie and Lawes, 2009a). This finding, combined with the continuous regeneration of *P. latifolius* during the angiosperm phase, results in a multi-aged *P. latifolius* canopy at the old-growth phase, which eliminates synchronous canopy senescence and the associated progressive overstory collapse (Adie and Lawes, 2009b). Second, angiosperm canopy trees in Afromontane forests are relatively shade intolerant, resulting in very limited angiosperm regeneration in

old-growth forest. Finally, gap creation, frequently caused by multiple tree falls, provides angiosperms with a limited opportunity of reaching the canopy in old-growth forest.

SUMMARY

Members of the Podocarpaceae, especially *P. latifolius*, are exceptionally successful in South African inland forests. The genus was decimated by colonial logging, and its present abundance in forest throughout its range is largely a consequence of that disturbance. Given adequate time, and in the absence of further catastrophic disturbance, *Podocarpus* will dominate the angiosperm flora. *Podocarpus* dominance is attributed to its longevity (Lawes et al., 2006) and ability to regenerate in shade, where all potential competing angiosperms are less capable of doing so (Adie and Lawes, 2009b).

To explain the geographical distribution of podocarps in South Africa, Midgley et al. (1995a) proposed that competitively superior angiosperms limit conifers in the more productive tropical environments. Indirectly, this claim holds in that deeply shaded habitat, resulting from higher angiosperm productivity, suppresses growth of *P. latifolius* seedlings. However, we found no evidence for direct competitive interaction between angiosperms and podocarps at the regeneration phase, with angiosperms appearing to be equally suppressed by the shaded conditions. We contend that the response by *P. latifolius* to light is the dominant and ultimate factor explaining the relatively poor performance of the conifer in scarp forest. Thus, the persistence of *P. latifolius* in this productive subtropical forest type is driven by disturbance that creates elevated light levels. Canopy gaps, however, do not facilitate *P. latifolius* regeneration in coastal scarp forests (e.g., Ongoye) because gaps are rapidly colonized by fast-growing vines (e.g., *Flagellaria guineensis*) that suppress canopy tree regeneration. Catastrophic disturbance, linked with the general longevity of podocarps, may offer one mechanism driving persistence.

We have no reason to suggest that African podocarps behave differently from other members of the Podocarpaceae. Rather, the prevalence of a generalist life history among competing angiosperms is important, and it is within this context that African podocarp ecology needs to be evaluated. African podocarps and their associated angiosperm flora have been shaped by Pleistocene climatic fluctuations. During the relatively benign interglacials that favored angiosperms, podocarps persisted by retreating to

their ancestral temperate zone refuges in montane regions. The intervening cold glacial periods drove podocarp expansion into lowland habitats, where they were able to compete successfully with angiosperms. African podocarps are thus temperate forest relicts and are not lowland rainforest survivors. The regression of Afrotemperate forest is likely to have placed floras under increasing risk of extinction by processes associated with fragmentation and those operating in the grassland matrix causing widespread species filtering that left a temperate angiosperm flora bereft of shade-tolerant species (Adie and Lawes, 2009b). *Podocarpus latifolius* is capable of establishing in relatively high light conditions and does not suffer the same constraints that place shade-tolerant species at risk of extinction in a fragmented landscape. The resulting relative difference in shade tolerance between conifers and angiosperms is an important determinant of forest structure and dynamics in Africa.

FUTURE RESEARCH DIRECTIONS

1. Palynological studies are needed to differentiate between *Afrocarpus* and *Podocarpus* to test the hypothesis that the present distribution of *Afrocarpus* is old (pre-Pliocene) whereas the more vagile *Podocarpus* is more recent (Pleistocene), reflecting rapid colonization followed by local extinction. *Podocarpus*, the older lineage compared with *Afrocarpus* (Biffin et al., this volume), is widespread in Africa, perhaps because of life history traits that promote dispersal, but local extinctions suggest the taxon is susceptible to climatic upheavals. It is tempting to suggest that the variable climate associated with volcanism and rifting in East Africa (Pik et al., 2008) and cooling (Kender et al., 2009) in the early to mid-Miocene led to the selection of traits that reinforced persistence but compromised dispersal ability in *Afrocarpus*. Recent research on the Maputaland coastal plain (northeastern South Africa) documents expansion and regression of podocarp forest (Mazus, 2000; Finch and Hill, 2008; Neumann et al., 2008). It is not clear whether the species represented in the pollen record is *A. falcatus*, present in lowland forest on the coastal plain, or *P. latifolius*, found in scarp forest just inland of the coast.

2. *Podocarpus latifolius* is the dominant species at altitude (inland mountains), where it dominates canopies. The mechanisms suppressing their performance in coastal scarp sites require examination, which will provide insight into why this species was unable to persist once lowland

forest extended its distribution following relaxation of glacial maxima (West Africa).

3. In spite of intensive colonial logging, *A. falcatus* has persisted and continues to be successful in forest habitats from the coastal lowlands to temperate highlands. Understanding the persistence of this species is particularly relevant in the face of severe logging pressure elsewhere in Africa (Wubet et al., 2003, 2006) and also as a window to the potential response of podocarps to climate change. Superior drought resistance (cf. Brodribb and Hill, 1998) may explain the persistence of *A. falcatus* on the coast in place of *P. latifolius*. The performance of *A. falcatus* under varying light and soil moisture and nutrient conditions requires testing, as we have done for *P. latifolius*.

4. The proposed long-term persistence of *A. falcatus* relative to *P. latifolius* may result from their contrasting reproductive biology and seed physiology. *Afrocarpus falcatus* is a dioecious masting species with a periodicity of six to seven years between reproductive events (Geldenhuys, 1993). *Podocarpus latifolius*, on the other hand, is an annual seeder, resulting in less episodic recruitment and lower vulnerability to climatic instability compared with *A. falcatus*, which may partly explain the wider and more continuous distribution of *P. latifolius*. In addition, shade-tolerant species rely on seed reserves for energy and nitrogen (Kitajima, 2002), and large energy reserves enhance establishment (Kitajima and Fenner, 2000). The high lipid content of *A. falcatus* seed (20%; Wirminghaus et al., 2002) may contribute to the success of this species in shaded environments and in competition with grasses in old-growth podocarp-dominated forests. Trials testing relative germination and establishment success with competing C_3 grasses are required to test the persistence hypothesis.

5. The recovery by *A. falcatus* and *P. latifolius* after colonial logging activities differ markedly, and understanding this relationship may offer insight into differences in their ecology and distribution. In the Drakensberg Mountains the response by *A. falcatus* was slow, resulting in a relatively low abundance and restricted distribution compared with the dominance of *P. latifolius*.

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The Ecology of Podocarps in Tropical Montane Forests of Borneo: Distribution, Population Dynamics, and Soil Nutrient Acquisition

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ABSTRACT. We review the ecology of podocarps on various soil types in Borneo, largely relying on our studies conducted on Mount Kinabalu. Podocarps are generally abundant in montane forests, but their abundance varies with soil nutrient status, and they can occur in lowland forests where soil nutrients are scarce. These patterns suggest control by soil nutrients rather than by temperature. Analyses of population structure, growth rate, and crown light conditions in montane forests indicate that podocarps are generally shade intolerant and require canopy gaps or sparse canopy for regeneration. Podocarps have greater maximum tree sizes than most co-occurring angiosperm species in Mount Kinabalu forests. Once they reach the upper canopy layer, they persist for a long time because of their long life span, allowing them to regenerate in rare events of canopy disturbance. The roots of two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) showed a greater acid phosphatase activity when compared with angiosperm roots within the same lower montane forest. Moreover, an analysis using lipid biomarkers indicated that saprophytic fungi are more abundant in the soils beneath the two podocarps than beneath angiosperms, and a fungal biomarker lipid correlated with soil acid phosphatase activity. The dominance of saprophytic fungi appears to be related to high soil acid phosphatase activity, suggesting feedback effects between the podocarps and soil microbial communities. These results indicate that podocarps are efficient in the acquisition of phosphorus from the acidic montane soils and decomposing litter. We suggest that the architectural and life history advantages and physiological adaptations to nutrient limitation are essential for the persistence of podocarps, despite their lower shade tolerance as compared to angiosperms.

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INTRODUCTION

The contemporary landscapes of Borneo are characterized by towering, evergreen broad-leaved tropical rainforests. Because the family Dipterocarpaceae is the dominant element, they are called mixed dipterocarp forest (Richards, 1996). The Gnetaceae, usually lianas, is the only gymnosperm family that is relatively common in such mixed dipterocarp forests. Because families in the Coniferales are virtually absent in mixed dipterocarp forests, plant ecologists may have the false impression that conifers are not physiologically adaptive to hot tropical climates. Richards (1996) illustrated that the Coniferales, including the Podocarpaceae, increases in abundance with increasing altitude in the paleotropics (Africa and South-east Asia, including New Guinea). Similarly, Veblen et al. (2005) stated that podocarps were generally restricted to montane cloud forests in tropical South America.

Although the patterns illustrated by Richards (1996) and Veblen et al. (2005) are real, they do not necessarily mean that the Podocarpaceae is a cool-climate element in the tropics, because soil nutrients may affect its distribution. There is a general trend in the tropics that lowland forests are limited by phosphorus availability and montane forests by nitrogen availability; in particular, soil nitrogen availability declines with increasing altitude, reflecting slower rates of mineralization (Tanner et al., 1998). Thus, it is not obvious that temperature, rather than nutrients, most strongly limits the distribution of the Podocarpaceae. In this review we illustrate the distribution patterns of the Podocarpaceae (and associated taxa) on various soil types in Borneo and suggest that they are controlled by soil nutrients more than by temperature. Our model site is Mount Kinabalu (Figure 6.1) in Sabah, a Malaysian state found in the north tip of Borneo.

Mount Kinabalu (4,095 m, 06°05'N, 116°33'E) is nonvolcanic and is the highest mountain in Southeast Asia between the Himalayas and New Guinea. The summit and adjacent areas are protected within the Kinabalu Park. Diverse pristine rainforests, which are all evergreen, occur from 300 m to the forest limit at 3,700 m (Kitayama, 1992a). The climate is humid tropical, with a weak influence of the Asiatic monsoon. Mean annual air temperature is 18.3°C at 1,560 m and decreases linearly with increasing altitude, with a mean lapse rate of 0.55°C per 100 m (Kitayama, 1992a). Month-to-month thermal seasonality is generally <2°C. Mean atmospheric saturation deficits become less negative upslope as a function of decreasing air temperature. Mean annual rainfall during 1994–1997 was approximately 2,300 mm at all altitudes. Longer-term

measurements may, however, demonstrate a much greater year-to-year variation in rainfall.

The geological substrates below 3,000 m consist of large areas of Tertiary sedimentary rocks with mosaics of ultramafic rocks (Jacobson, 1970). The folding of the sedimentary rocks occurred in the middle Miocene (15 MYA), and the ultramafic rocks were probably up-faulted into the sedimentary rocks at that time. The summit area above 3,000 m consists of granitic (adamellite) rocks. The intrusion of the batholithic granite through sedimentary rocks started in the upper Miocene (7–9 MYA), and the summit is still being uplifted. The ultramafic rocks are remarkably high in magnesium and low in phosphorus compared with sedimentary and granitic rocks found in the area.

Forest ecosystems of Mount Kinabalu were recently investigated intensively with permanent plots at various altitudes on different surface geologies (Kitayama et al., 1998, 2004; Aiba and Kitayama, 1999; Kitayama and Aiba, 2002; Takyu et al., 2002; Aiba et al., 2004, 2005, 2006, 2007; T. Seino and K. Kitayama, unpublished). Forest function, nutrient dynamics, and the populations of all trees >5 cm in diameter at breast height (dbh) were investigated (Table 6.1). In this paper, we review the results pertinent to the Podocarpaceae on Mount Kinabalu.

The genus *Phyllocladus* is included in Podocarpaceae in this paper (see Biffin et al., this volume), although it has been elevated to family level in some of the literature (Page, 1990; Bobrov et al., 1999). Podocarpaceae forms a monophyletic lineage with Araucariaceae within extant conifer families in the molecular phylogeny; both families possess nodulelike structures on roots and show a geographic distribution biased to the Southern Hemisphere, probably reflecting their Gondwanan origins (Quinn et al., 2002). All coniferous species occurring on Mount Kinabalu belong to these two families. We therefore include Araucariaceae (only the genus *Agathis* occurs in Borneo) in places because the two families are likely to share some common ecological characteristics owing to their common ancestry.

DISTRIBUTIONAL PATTERN

GENERAL ALTITUDINAL DISTRIBUTION

In the lower montane tropical rainforest at park headquarters (1,560 m) of Kinabalu Park, one can easily recognize slightly overtopping crowns of conifers by their fine texture (Figure 6.2). These conifers are likely to be either of the two abundant podocarps, *Dacrycarpus imbricatus* and *Dacrydium gracile*. The other dominant



FIGURE 6.1. Mount Kinabalu viewed from the park headquarters (1,560 m) on the south slope.

species include angiosperm trees of the genera *Tristania*, *Syzygium* (both Myrtaceae), and *Lithocarpus* (Fagaceae). Similar forests characterized by the dominance of conifers (especially podocarps) are seen in montane forests (subalpine, upper montane, and lower montane forests; Kitayama, 1992a) on Mount Kinabalu above the upper limit (1,200 m) of mixed dipterocarp forest. A total of 20 species of conifer (three Araucariaceae and 17 Podocarpaceae, including one *Phyllocladus*) have been recorded on Mount Kinabalu (Beaman and Beaman, 1998).

Conifers have long been considered an important "montane" floristic element on Mount Kinabalu (van Steenis, 1964; Meijer, 1965). Quantitative analysis of the vegetation on zonal soils from the lowlands to the upper limit of forest (600–3,400 m) supported this general

pattern: podocarps and other conifers were recorded only at $\geq 1,400$ m (Kitayama, 1992a). Podocarps were notably dominant from 2,800 to 3,400 m (Kitayama, 1992b), although the number of podocarp species peaked at 1,500–1,600 m (Beaman and Beaman, 1998). Therefore, at first glance, the distribution of podocarps appears to be controlled by climate (primarily by temperature).

Analyses of the altitudinal distribution patterns of trees on different geological substrates on Mount Kinabalu (Aiba and Kitayama, 1999), however, suggest that the occurrence of podocarps is, in reality, controlled by a more complex interaction of climate and soil conditions (Figure 6.3). The abundance of podocarps at a site generally increases with altitude, but it can vary from site to site depending on geology. As has been stated, on zonal

TABLE 6.1. Description of sample plots established on different geological substrates on Mount Kinabalu.

Exact elevation (m)	Area (ha)	Tree density (ha ⁻¹) ^a	Altitudinal zone ^b	Surface geology ^c	Topography ^d	Census year	Reference
Nonultramafic rock (zonal soil)							
650	1.00	1,055 ^e	L	T	S	1996	Aiba and Kitayama (1999)
1,560	1.50 ^f	1,921	LM	T	L	1997, 2002	Takyu et al. (2002), Kitayama et al. (2004), Aiba et al. (2006)
1,560	0.10	3,030	LM	T	M	1997	Takyu et al. (2002)
1,560	0.05	3,300	LM	T	R	1997	Takyu et al. (2002)
1,860	1.00	1,951	LM	Q	L	1996	Takyu et al. (2002), Kitayama et al. (2004)
1,860	0.10	2,450	LM	Q	M	1997	Takyu et al. (2002)
1,860	0.05	3,180	LM	Q	R	1997	Takyu et al. (2002)
1,950	0.50	1,624	LM	T ^g	V	2000	T. Seino and K. Kitayama (unpublished)
2,590	0.25	2,116	UM	T	S	1995	Aiba and Kitayama (1999)
3,080	0.20	3,665	SA	G	S	1995	Aiba and Kitayama (1999)
Ultramafic rock (azonal soil)							
700	1.00	1,195 ^e	L	S	S	1996	Aiba and Kitayama (1999)
1,860	0.20	3,445	LM	S	L	1995	Aiba and Kitayama (1999), Takyu et al. (2002)
1,860	0.10	4,190	LM	S	M	1997	Takyu et al. (2002)
1,860	0.05	4,100	LM	S	R	1997	Takyu et al. (2002)
2,700	0.20	3,775	UM	S	S	1995	Aiba and Kitayama (1999)
3,050	0.06	4,383	SA	S	S	1995	Aiba and Kitayama (1999)

^a Stems ≥5 cm diameter at breast height.^b L, lowland; LM, lower montane; UM, upper montane; SA, subalpine zones (Kitayama, 1992a).^c T, Tertiary sedimentary rock; Q, Quaternary sediment; G, granite; S, serpentine rock.^d L, lower slope; M, middle slope; R, ridge top; S, side slope; V, valley bottom.^e Estimates based on the entire plot (1 ha) for stems ≥10 cm diameter at breast height and subsamples (0.20 ha) for stems <10 cm diameter at breast height.^f A single 1-ha plot censused in 1997 and two 0.25-ha plots censused in 2002.^g The surface geology of this site appears to include various rock types (Quaternary sediment and ultramafic rock), although the site is mapped within an area of Tertiary sedimentary rock in Jacobson (1970).

soils derived from sedimentary or granitic rocks, the genera *Dacrycarpus* and *Dacrydium* are the dominant podocarps in the most developed forests on gentle slopes in the montane zone or above. Podocarps, which are otherwise exclusively montane, occur at a lower altitude of 700 m on soils derived from ultramafic rock, suggesting that soil conditions can strongly influence their distribution. The phylogenetically associated family Araucariaceae (*Agathis borneensis* in lowland forests and *A. kinabaluensis* in montane forests) also demonstrates a staggered, lowered altitudinal distribution on soils derived from ultramafic rock.

Podocarps and *Agathis borneensis* can occur at sea level in Borneo on sandy or swampy soils (de Laubenfels, 1988; Miyamoto et al., 2003; Nishimura et al., 2007). A low-stature evergreen forest, consisting of slender gnarled

trees, occurs on nutrient-impooverished, sandy Spodosols (Soil Survey Staff, 1999), and the forest is termed "heath forest." In the southwestern lowlands of interior Sabah, *Dacrydium pectinatum* is among the dominant species of heath forest at 500 m (Figure 6.4). The relative basal area of *Dacrydium* can exceed 40%, and Myrtaceae and Dipterocarpaceae compose the bulk of the rest in this forest (K. Takahashi and K. Kitayama, Kyoto University, unpublished data). This again suggests that the altitudinal distribution of podocarps is "lowered" on nutrient-impooverished soils.

All of the podocarp species (as well as *Agathis* species) have broad altitudinal ranges on Mount Kinabalu. *Dacrycarpus imbricatus* was once believed to occur from 1,400 up to 4,000 m. After a taxonomic revision, however, the



FIGURE 6.2. The canopy of lower montane tropical rainforest on Mount Kinabalu at 1,560 m, where several of the studies described in this chapter were conducted. This forest is dominated by *Dacrycarpus imbricatus* and *Dacrydium gracile*.

plants at the upper slope were split as an endemic species, *D. kinabaluensis*. The latter species occurs most abundantly (with 5% relative basal area or greater) at altitudes higher than 2,800 m on both ultramafic and sedimentary rocks (Kitayama, 1992a; Aiba and Kitayama, 1999). Five species of *Dacrydium* occur between 800 and 3,700 m (Beaman and Beaman, 1998; although occurrence of one species is questionable). *Phyllocladus hypophyllus* also occurs widely from 1,200 up to 4,000 m. These distribution patterns suggest that podocarps have potentially wide physiological ranges. Three species of *Agathis* (Araucariaceae) are recorded from the somewhat narrower range from 800 to 2,200 m.

Although podocarps (the genera *Dacrycarpus* and *Dacrydium* in particular) have a potentially wide altitudinal range, there is a distribution gap between 2,000 and 2,800 m on gentle slopes on sedimentary soils (corresponding to the upper montane tropical rainforest) where *Dacrycarpus* does not occur (Kitayama, 1992a). Aiba and Kitayama (1999) also found only one podocarp species (*Phyllocladus hypophyllus*) in an upper montane cloud forest on sedimentary soils at 2,590 m. The soils in the upper montane forest are commonly waterlogged and chemically reduced because of persistent cloud and rainfall and may be too wet for the other conifers. Indeed, podocarps can frequently occur on steep ridges on sedimentary rock

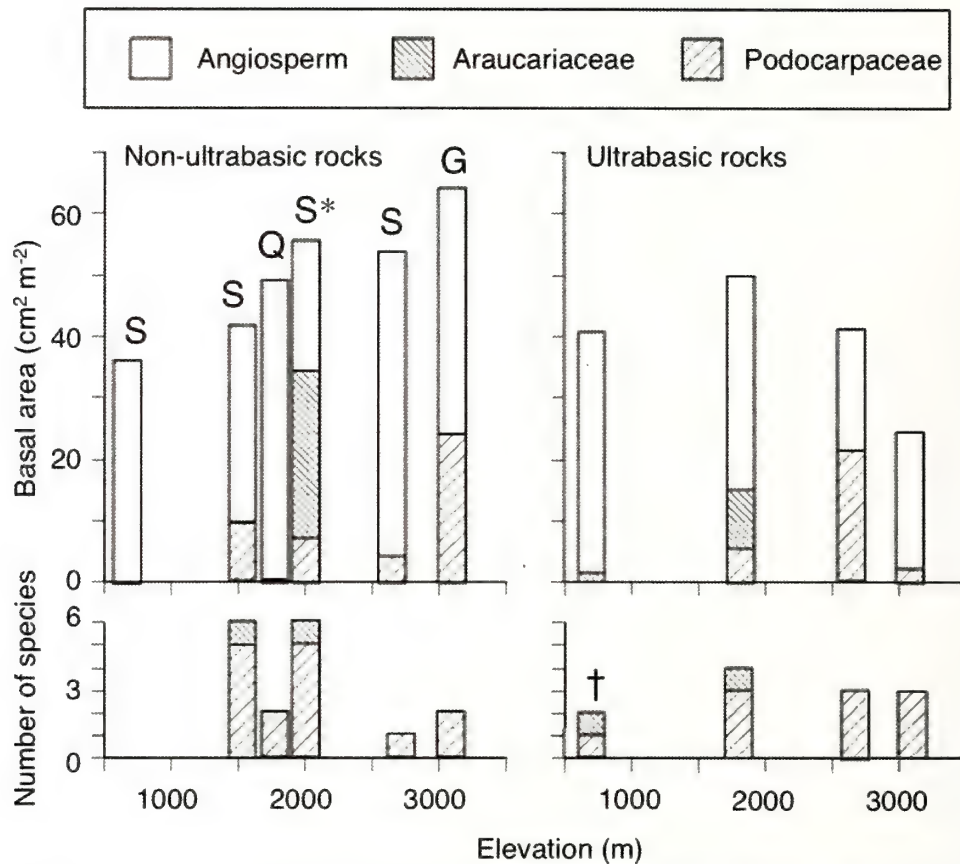


FIGURE 6.3. (top) Basal area and (bottom) number of species of conifer families (Podocarpaceae and Araucariaceae) for trees ≥ 5 cm diameter at breast height in sample plots on side slopes (including lower slopes and valley bottom) established on two geological substrates along elevational gradients on Mount Kinabalu. The basal area of angiosperm trees combined is also shown. Rock types are indicated for nonultramafic series as follows: S = Tertiary sedimentary rock, Q = Quaternary sediments, G = granite. The surface geology of the site indicated by an asterisk (*) may include various rock types; see footnote g of Table 6.1. The number of species for the plot at 700 m on ultramafic rock [indicated by a dagger (†)] includes one podocarp species that occurs just outside the plot (*Dacrycarpus imbricatus*).

or gentle slopes on ultramafic rock in this zone (Kitayama, 1995). At these sites, water permeability is high because of steep topography and, on ultramafic soils, the presence of iron oxides, which have a low affinity with water. *Dacrycarpus* gains dominance in the slightly drier subalpine zone ($\geq 2,800$ m), which is above the persistent cloud. *Dacrydium* occurs in low abundance in the lower montane zone but does not occur in the upper zone except on ridgetops and ultramafic soils. As explained above, podocarps do occur on waterlogged soils elsewhere in Borneo, and we do not know why they are absent from such soils on Mount Kinabalu.

Although conifers co-occur with angiosperms, the “additive basal area phenomenon” (Enright and Ogden, 1995; Aiba et al., 2007) is not evident on Mount Kinabalu. This phenomenon is often reported for mixed conifer–angiosperm forests in the Southern Hemisphere, in which the high basal area of conifers does not cause the reduction of basal area of angiosperms.

RESPONSE TO VARIATION IN SOIL NUTRIENTS

The above description suggests that soil conditions rather than climate may impose the main control



FIGURE 6.4. Heath forest on white silica sands in the interior of Sabah, north Borneo, at 500 m. *Dacrydium pectinatum* is the dominant species in this nutrient-impo-
verished forest.

on the occurrence of podocarps and other conifers on Mount Kinabalu. Variation in podocarp abundance appears to be correlated with net soil nitrogen mineralization rate (Figure 6.5). Takyu et al. (2002) investigated tree species composition in nine lower montane forests at 1,560–1,860 m on Mount Kinabalu, including ridge, middle-slope, and lower-slope forests, each occurring on unconsolidated Quaternary sediment (colluvial deposits of sedimentary rocks), Tertiary sedimentary rock, and ultramafic rock (Table 6.1). Soil nitrogen availability generally decreases from Quaternary to Tertiary to ultramafic (most nutrient deficient) and from lower slope to middle slope to ridge (most nutrient deficient) on each substrate.

With this combination of site conditions, the abundance of podocarps generally decreases with increasing nitrogen availability ($r = -0.47$, $p = 0.203$), significantly so when all conifers (including *Agathis*) were included ($r = -0.67$, $p = 0.049$). It has been demonstrated that soil phosphorus availability also changes with geological substrate and topography in a manner similar to soil nitrogen (Kitayama and Aiba, 2002; Kitayama et al., 2004). Therefore, nitrogen in concert with phosphorus may be important in determining the abundance of podocarps and other conifers in the lower montane zone of Mount Kinabalu.

Kitayama et al. (2004) compared soil phosphorus availability in two lower montane tropical rainforests with

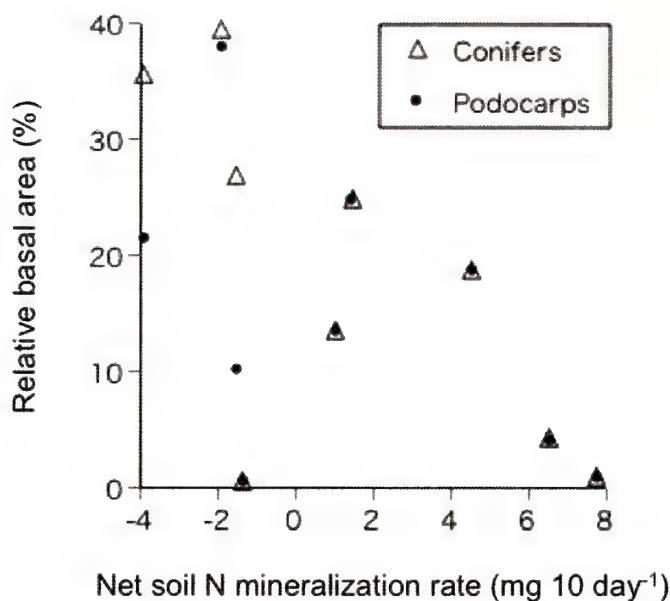


FIGURE 6.5. The relationships between net soil nitrogen mineralization rate and the relative basal areas of podocarp and conifer species in nine tropical rainforests of the lower montane zone on Mount Kinabalu. Net soil nitrogen mineralization rate was determined by 10-day incubation of forest soils in polyethylene bags (Takyu et al., 2002).

similar air temperature regimes but on different geological substrates: highly weathered soils on stable, old Tertiary sedimentary rocks and undeveloped soils on unconsolidated Quaternary sediment (Table 6.1). Concentrations of labile and total phosphorus were much lower in the old soils and appeared to control primary productivity. Podocarps are among the dominant trees in forests growing on old soils but are very rare in the forest growing on young soils, suggesting that phosphorus availability alone or in concert with nitrogen availability controlled the occurrence of podocarps at these sites.

POPULATION ECOLOGY IN MONTANE FORESTS

DIAMETER DISTRIBUTION

In the montane (and subalpine) forests on Mount Kinabalu, podocarps and the associated conifer *Agathis kinabaluensis* do not necessarily appear to be competitive with angiosperm trees in terms of aboveground competition for light. Figure 6.6 demonstrates the diameter size

class distribution of conifers (podocarps and *A. kinabaluensis*) and angiosperm trees in three upland forests on zonal soils derived from sedimentary or granitic rocks and two forests on soils derived from ultramafic rocks. Conifers are minor elements in terms of the number of stems, but they constitute a substantial fraction of large-sized stems, resulting in a relatively large basal area (Figure 6.3). Individual conifer species usually show flat or monomodal diameter distributions with few small trees, which indicates that they are shade intolerant (Figure 6.7). Occasionally, some conifers show an L-shaped diameter distribution with abundant small trees. However, the canopy layers in such forests are sparse, which allows smaller conifer trees to persist in the understory layer. These cases are rather rare. *Dacrycarpus kinabaluensis* found at 3,080 m on granite showed extremely unimodal diameter distribution, which might reflect an episodic recruitment following large-scale disturbance (e.g., El Niño-related drought or landslides). *Falcatifolium falciforme* at 1,560 m on sedimentary rock is exceptional in that it shows clearly an L-shaped diameter distribution and saplings grow abundantly in shaded conditions of the forest understory (see below).

DIAMETER GROWTH RATE AND CROWN LIGHT CONDITION

A detailed study of growth and crown conditions for 42 abundant tree species was conducted for stems ≥ 10 cm dbh in the lower montane forest at 1,560 m on sedimentary rock (Aiba et al., 2004, 2006). These species include four conifers (all podocarps) and 38 angiosperms. The study involved the investigation of overshading of each individual and its growth rate. The condition of overshading was expressed as a crown position index, which ranges from 1 (fully lit condition without any portion of neighboring crowns above that tree) to 4 (fully shaded by neighboring crowns above that tree). Podocarps other than *Falcatifolium falciforme* were characterized by well-lit crowns and high trunk diameter growth rates (Figure 6.8). These characteristics suggest that in this forest podocarps are light-demanding, relatively fast-growing species that require canopy gaps (e.g., by tree fall and slope failure) for regeneration and that in closed-canopy forests they are competitively inferior to angiosperms that are generally more shade tolerant. It is expected that podocarps would be eliminated from the forest in the absence of canopy disturbance.

Frequent disturbance might allow podocarps to persist in montane forest on Mount Kinabalu despite their

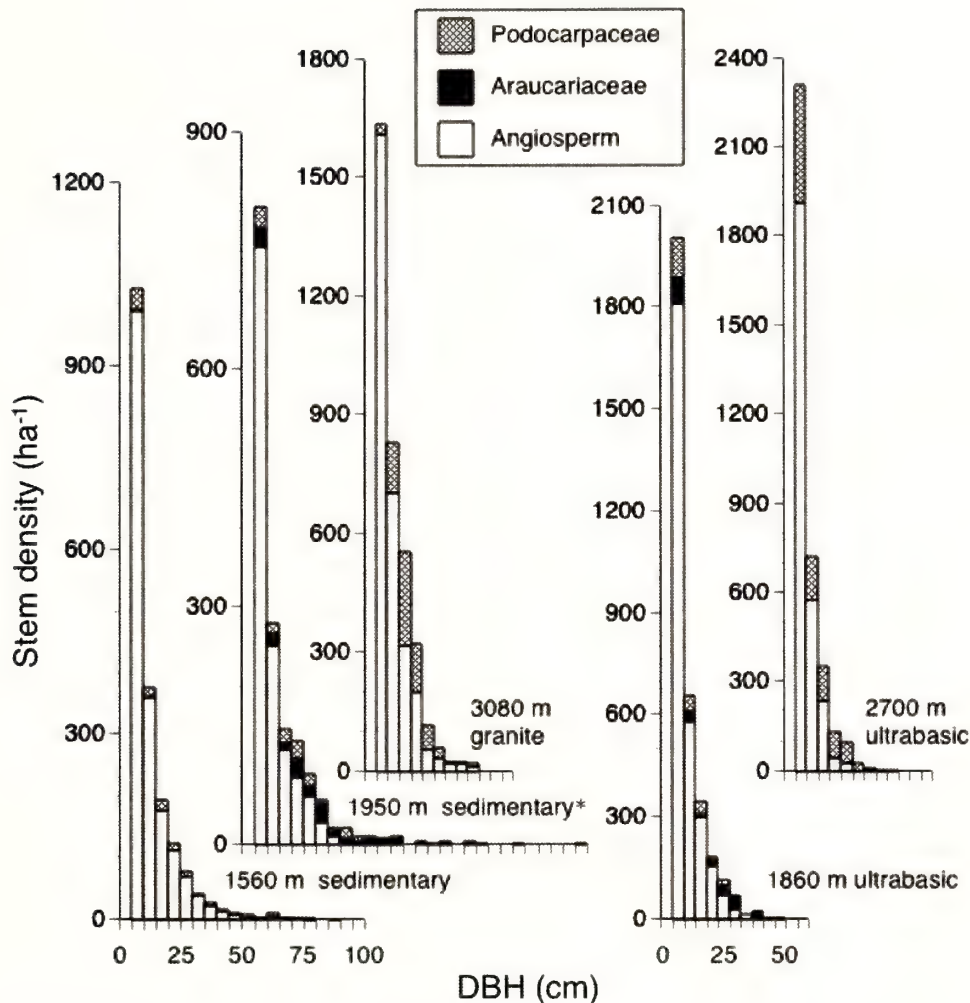


FIGURE 6.6. Diameter distribution of conifers (Podocarpaceae and Araucariaceae) and angiosperm trees in the sample plots where conifers attain dominance at various altitudes on different geological substrates. Note that the scales of the vertical axis differ among plots. The site indicated by an asterisk (*) appears to include various rock types; see footnote g of Table 6.1.

inferiority to angiosperms in shade tolerance. However, montane (and subalpine) forests are generally less dynamic than lowland forests on Mount Kinabalu in terms of population turnover rate (Aiba et al., 2005), suggesting less-frequent disturbance at higher elevations. This characteristic seems to be true even when irregular droughts associated with El Niño, which have inflated tree mortality, especially at higher elevations, are taken into account. Podocarps grow slowly because of light limitation in the forest understory. They can successfully regenerate only in well-lit conditions, but angiosperm pioneers of such genera as *Macaranga* and *Ficus* presumably outcompete podocarps on nutrient-rich soils. Only on the nutrient-deficient

soils in the montane forest where angiosperms grow slowly because of nutrient limitation can podocarps outcompete angiosperm pioneers.

ADVANTAGES AND ADAPTATIONS

In the above two sections, we described the distribution patterns, population structure, and growth rate of podocarps in the mixed evergreen conifer–broad-leaved tropical rainforests on Mount Kinabalu. Evidence suggests that podocarps have a wide temperature range (physiological niche) but are competitively inferior to co-occurring

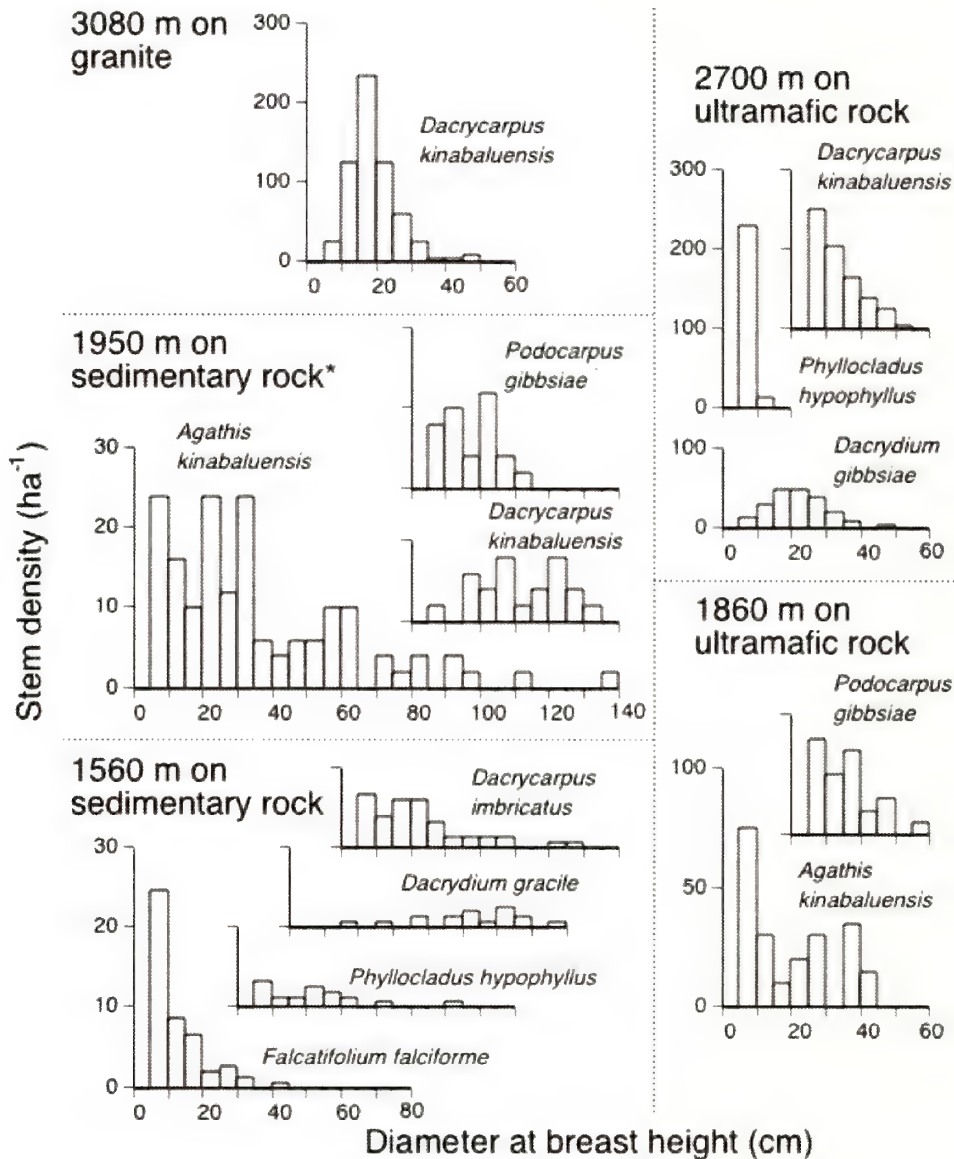


FIGURE 6.7. Diameter distribution of abundant conifers (sample size ≥ 15) in the sample plots where conifers attain dominance. All species belong to Podocarpaceae except for *Agathis kinabaluensis* (Araucariaceae). Note that the scales of the vertical axis differ among plots. The site indicated by an asterisk (*) appears to include various rock types; see footnote g of Table 6.1.

angiosperms, particularly in competition for light. It seems that when the availability of soil nutrients (nitrogen and/or phosphorus) is limited, podocarps can outcompete co-occurring angiosperms. In the following section, we discuss the architectural and life history advantages and the physiological adaptations to such nutrient limitation that allow podocarps to persist in the contemporary landscapes of the Bornean tropics.

ARCHITECTURAL AND LIFE HISTORY ADVANTAGES

Podocarps consistently form an uppermost canopy layer in the lower montane forest of Mount Kinabalu, giving an impression of their predominance. The formation of such an upper layer is not a transient process but contributes to a persistent forest structure based on their architectural traits. Figure 6.9 shows dbh–height relationships

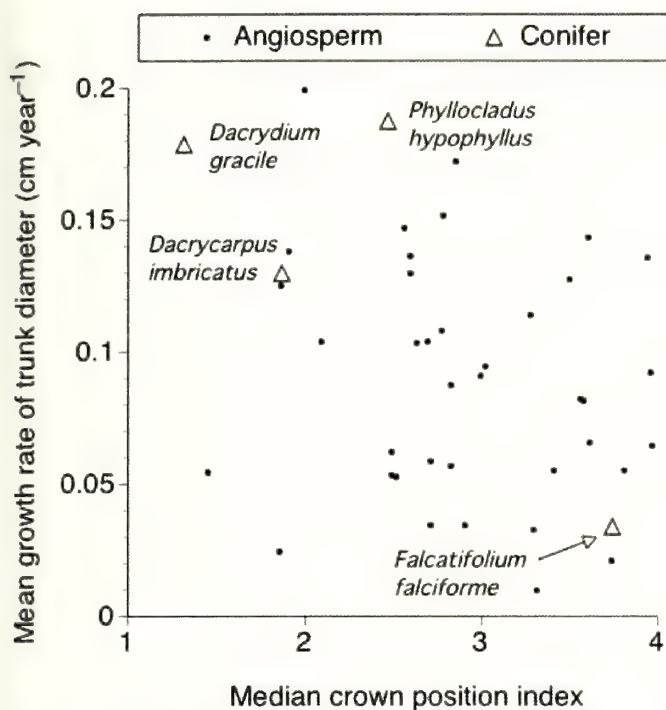


FIGURE 6.8. The relationship between median crown position index (CPI) and mean diameter growth rate at 10–40 cm diameter at breast height among 42 abundant tree species in a tropical montane forest plot at 1,560 m on sedimentary rock. Triangles indicate conifers (all Podocarpaceae), and dots indicate angiosperms. Low median CPI indicates that species are characterized by well-lit crowns in heterogeneous canopy structure. Modified from Aiba et al. (2004, 2006).

among co-occurring podocarps (*Dacrycarpus kinabaluensis*, *Dacrydium gibbsiae*, and *Phyllocladus hypophyllum*), associated *Agathis kinabaluensis*, and angiosperms in the lower montane forest at 1,950 m on “sedimentary” rock (see footnote g of Table 6.1). Two dominant conifers (*Dacrycarpus* and *Agathis*) attained a greater size in terms of both diameter and height than angiosperm trees. Moreover, when dbh–height relationships (log-transformed) were analyzed by analysis of covariance, the intercepts differed between conifers and angiosperms, and conifers were taller than angiosperm trees at a given diameter (Aiba et al., 2007). Thus, shade-intolerant conifers can survive in the forest by occupying an upper canopy layer where they can receive much sunlight.

For the above forest, we also estimated turnover time of the two dominant conifers *Dacrycarpus kinabaluensis* and *Agathis kinabaluensis* from the increase in basal area of surviving trees over nine years (2000–2009), assuming

that basal areas of individual species are in equilibrium (i.e., an increase in growth is balanced by a decrease in death if a sufficiently long period is considered). The turnover times of conifers were 168 years for *Dacrycarpus* and 364 years for *Agathis*, which were substantially longer than those of angiosperm trees (mean of 105 years for all species combined). Bornean conifers can therefore be regarded as long-lived trees that have many opportunities to regenerate during their life spans.

ACQUISITION OF PHOSPHORUS: ACID PHOSPHATASE ACTIVITY OF PODOCARP ROOTS

The soils of the tropical lower montane forests on sedimentary rock on Mount Kinabalu (where podocarps often become dominant) are broadly categorized as Spodosols, which are highly acidic (pH 3.1–4.0 in the surface horizon) and impoverished in soluble inorganic forms of phosphorus and nitrogen (Kitayama et al., 1998; Kitayama and Aiba, 2002). Kitayama et al. (2004) demonstrated that soils in the lower montane zone where podocarps were abundant were characterized by much lower total phosphorus concentrations than areas in the same zone where podocarps were rare. Further, phosphorus fractionation revealed that soil phosphorus at sites where podocarps were abundant consisted of a high proportion of physically occluded inorganic phosphate and refractory organic phosphorus, with low concentrations of labile organic phosphorus. On such soils, tree species that can acquire phosphorus from fresh litter or can scavenge labile organic phosphorus from the surface horizon may have a competitive advantage because the solubility of inorganic phosphorus fractions is extremely low. Phosphatase enzymes are required to hydrolyze phosphate from organic phosphorus in litter or soil. Phosphatases are excreted by tree roots and, in plants such as the Fagaceae, by symbiotic ectomycorrhizal fungi.

Y. Fujiki and K. Kitayama (unpublished) investigated acid phosphatase activity on roots systematically for all top to middle dominant species across three forests with differing soil phosphorus availability in the lower montane zone (1,560–1,860 m) on Mount Kinabalu. The analysis was conducted on fresh roots of seedlings of podocarps and 23 angiosperm species (Fagaceae, Myrtaceae, and other families). It should be noted that in the Fagaceae the phosphatase activity of symbiotic ectomycorrhizas is also likely to have been included in the root measurements. Roots were excavated, transported to the laboratory in a cooler box, rinsed with pure water, and assayed with *para*-nitrophenyl phosphate (a chromogenic phosphatase substrate) in acetate buffer (pH 5.0). The activity of

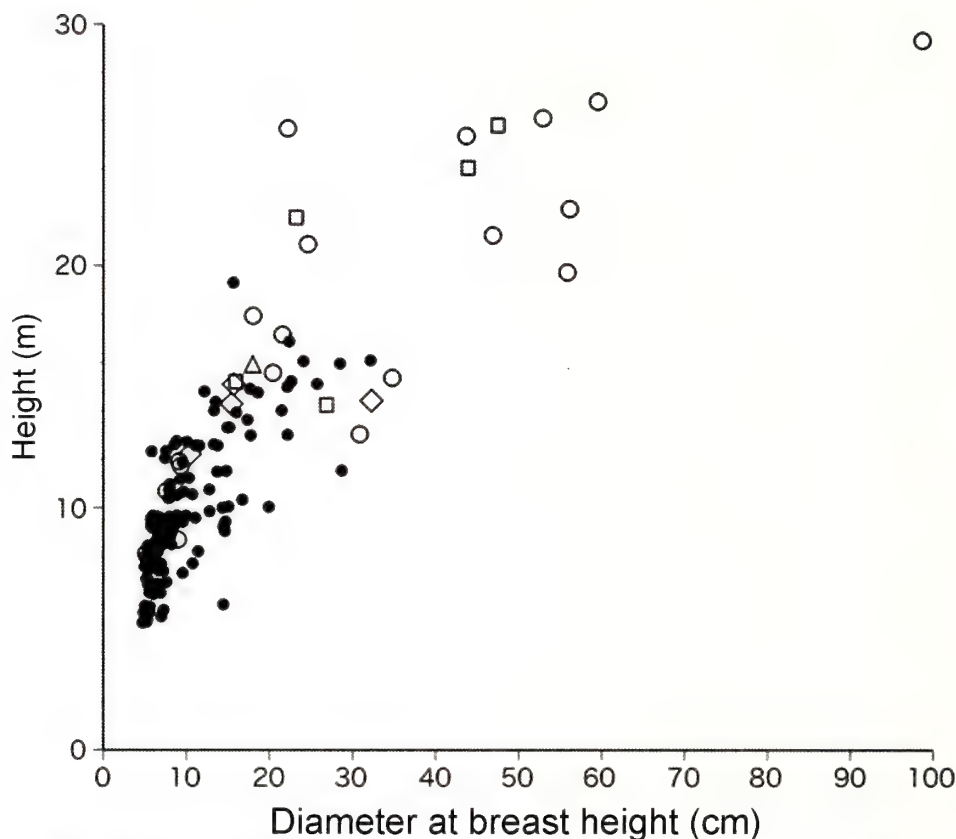


FIGURE 6.9. The relationship between diameter at breast height and tree height for conifers and angiosperms at 1,950 m on sedimentary rock (see footnote g of Table 6.1), measured in a 10 × 100 m transect laid in a sample plot. *Dacrycarpus kinabaluensis* (squares), *Podocarpus gibbsiae* (triangles), and *Phyllocladus hypophyllus* (diamonds) belong to Podocarpaceae, and *Agathis kinabaluensis* (circles) belongs to Araucariaceae. Black dots represent angiosperm trees.

phosphatase is expressed as the amount of product (*para*-nitrophenol) released per surface root area per unit time. The mean acid phosphatase activity on roots of Podocarpaceae (*Dacrycarpus imbricatus*, *Dacrydium gibbsiae*, *Dacrydium gracile*, *Phyllocladus hypophyllus*, and *Podocarpus gibbsiae*) was significantly greater than that of angiosperms (Figure 6.10, linear mixed model, $p = 0.03$).

The greater ability of podocarp roots to release phosphate from phosphomonoesters in organic matter may contribute to the efficient acquisition of phosphorus from litter and/or labile organic soil phosphorus fraction. This is potentially an important adaptation facilitating the persistence of podocarps on acidic montane Spodosols and is consistent with the depletion of inositol phosphate, a common phosphomonoester, as the abundance of podocarps increases in old soils along a temperate rainforest chronosequence in New Zealand (Turner et al., 2007). The same

mechanism is also advantageous on soils derived from ultramafic rocks, in which inorganic phosphate is depleted and, consequently, the contribution of organic phosphorus to plant nutrition is relatively important (Kitayama et al., 1998; Kitayama and Aiba, 2002).

SYMBIOTIC NITROGEN FIXATION

Earlier researchers speculated that podocarp roots had the ability to fix nitrogen because of the occurrence of nodule-like structures on the root surface (van Tieghem, 1870; Becking, 1965; Silvester and Bennett, 1973; Dickie and Holdaway, this volume). Roots of podocarp species (*Dacrycarpus imbricatus*, *Dacrydium gracile*, *Falcatifolium falciforme*, *Podocarpus gibbsiae*, and *Phyllocladus hypophyllus*) from the lower montane tropical rainforest at 1,560 m on sedimentary rock were assayed

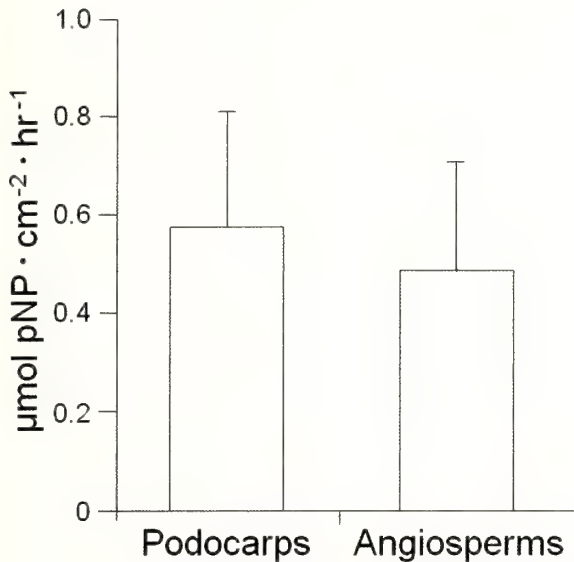


FIGURE 6.10. Mean (\pm standard deviation) acid phosphatase activity of the roots of podocarp species versus angiosperm species in the lower montane forests of Mount Kinabalu. Acid phosphatase activity is expressed as product (*para*-nitrophenol) released per root surface area per unit time. The effects of tree species taxa (i.e., podocarps versus angiosperms) on acid phosphatase activity were evaluated by a linear mixed model (acid phosphatase activity \sim taxa (podocarps or angiosperms), random effects = plant individuals).

for nitrogen-fixing ability by following the standard acetylene reduction assay of Hardy et al. (1973) (M. Ushio and K. Kitayama, unpublished). *Agathis kinabaluensis* was also included in the analysis. Significant ethylene production was not detected in all of these samples (data not shown); therefore, podocarps and *Agathis kinabaluensis* on Mount Kinabalu did not have nitrogen fixation ability (see also Dickie and Holdaway, this volume).

INFLUENCES OF PODOCARPS ON SAPROTROPHIC MICROBIAL COMMUNITIES

The abundance and composition of the soil microbial community can be affected by plant species through the chemical quality and quantity of their litter (Porazinska et al., 2003; Bartelt-Ryser et al., 2005; Kao-Kniffin and Balser, 2008). The two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) on Mount Kinabalu produce leaves in which the concentration of condensed tannins is relatively high compared to co-occurring broad-leaved species (S. Suzuki, Institute for Environmental Sciences, unpublished data). Condensed tannins can affect

the composition and abundance of the soil microbial community (Kraus et al., 2003). Therefore, it is possible that the podocarp species have impact through the effects of foliar condensed tannins on soil microbial communities, which in turn affect soil nutrient acquisition by podocarps.

Ushio et al. (2008) investigated the influences of podocarp litter on soil microbial communities in the lower montane forest on sedimentary rock at 1,560 m on Mount Kinabalu. Two podocarp species (*Dacrycarpus imbricatus* and *Dacrydium gracile*) had a distinct impact on the abundance and composition of soil microbial community (Table 6.2, Figure 6.11). Ushio et al. (2008) collected soil samples beneath five tree species (the two podocarps plus three angiosperms: *Lithocarpus clementianus*, *Palaquium rioense*, and *Tristanopsis* sp.) that were dominant in this forest. The total lipid abundance (a proxy for microbial biomass) was greater in soils underneath *Dacrydium* than soils underneath *Tristanopsis* ($p < 0.05$), and the abundance of specific indicator lipids also differed among some combinations of tree species (Table 6.2). The ratio of fungi to bacteria differed significantly between *Dacrycarpus* and *Lithocarpus*, between *Dacrydium* and *Lithocarpus*, and between *Dacrydium* and *Tristanopsis* ($p < 0.05$). The ratio of Gram+ to Gram- bacteria was significantly higher in the soils underneath *Dacrydium* than in the soils underneath *Tristanopsis* ($p < 0.05$).

A principal components analysis (the analysis of overall microbial composition) also indicated distinct species-specific effects of podocarps (Figure 6.11). *Dacrycarpus* and *Tristanopsis* ($p < 0.05$) and *Dacrydium* and *Tristanopsis* ($p < 0.01$) differed along PC1, whereas *Dacrycarpus* and *Lithocarpus* ($p < 0.01$) and *Dacrycarpus* and *Palaquium* ($p < 0.05$) differed along the PC2 axis. Thus, mean coordinates of *Dacrycarpus* and *Dacrydium* (both podocarp species) were not significantly different from each other, and they were different from the mean coordinates of *Tristanopsis*, *Lithocarpus*, and *Palaquium* (angiosperms). These results suggest that the primary difference in composition of soil microbial communities exist between conifer and angiosperm species, especially in terms of the relative dominance of saprophytic fungi.

In addition to the microbial compositions, Ushio et al. (2010) investigated the activity of acid phosphatase in soils. Since plant roots were carefully removed from soil before the measurements of soil enzyme activity, the results were thought to reflect the effects of the saprophytic microbial community. They found greater activity of acid phosphatase in the soils beneath *Dacrydium* than *Lithocarpus*. They also found a significant correlation between acid phosphatase and a fungal biomarker lipid (Ushio et al.,

TABLE 6.2. Mean abundance of indicator lipids in soils beneath dominant podocarp and angiosperm tree species in a lower montane forest at 1,560 m on Mount Kinabalu. Values within rows having the same superscripted lowercase letter are not significantly different by the Tukey–Kramer honestly significant difference test (for equal variance data) or the Games–Howell test (for unequal variance data) ($p < 0.05$). Gram+ bacteria are the sum of iso-branched and saturated lipids (i14:0, 15:0, i15:0, a15:0, i16:0, 17:0, i17:0, and a17:0), actinomycetes are the sum of methyl branched lipids (17:0 10Me and 19:0 10Me), and Gram– bacteria are the sum of mono-unsaturated and cyclopropyl lipids (16:1 ω 7, cy17:0, and cy19:0). Saprophytic fungi, ectomycorrhizas/saprophytic fungi, arbuscular mycorrhizas, and protozoa are indicated by the lipid abundance of 18:2 ω 6,9, 18:1 ω 9, 16:1 ω 5, and 18:3 ω 6,9,12, respectively. The fungi : bacteria ratio is the sum of abundance of fungal lipids (18:2 ω 6,9, 18:1 ω 9) to the sum of Gram+ and Gram– lipids shown here. The Gram+ : Gram– ratio is the ratio of the sum of iso- and methyl-branched lipids to the sum of monounsaturated and cyclopropyl lipids. Values in parentheses are the standard error of the mean. Data were modified from Ushio et al. (2008).

Measurement	Lipid abundance (nmol g ⁻¹)				
	<i>Dacrycarpus</i>	<i>Dacrydium</i>	<i>Lithocarpus</i>	<i>Palaquium</i>	<i>Tristaniaopsis</i>
Total lipid	1,617 ^{ab} (307)	2,309 ^a (240)	1,799 ^{ab} (336)	1,566 ^{ab} (346)	1,118 ^b (63)
Gram+ bacteria	170 (39.5)	231 (16.1)	213 (39.0)	185 (42.7)	139 (12.1)
Actinomycetes	24.1 ^a (2.7)	59.7 ^a (9.4)	52.9 ^a (13.2)	42.7 ^{ab} (16.7)	7.5 ^b (3.2)
Gram– bacteria	90.1 (15.9)	129 (6.4)	128 (22.6)	114 (21.2)	97.6 (8.7)
Saprophytic fungi	112 ^{ab} (17.0)	157 ^a (15.7)	99.5 ^{ab} (16.9)	93.9 ^{ab} (15.7)	76.6 ^b (5.9)
Ectomycorrhizas/saprophytic fungi	141 ^{ab} (30.8)	181 ^a (11.2)	144 ^{ab} (17.6)	119 ^{ab} (13.6)	101 ^b (8.9)
Arbuscular mycorrhizas	69.7 ^{ab} (13.5)	97.2 ^a (8.6)	69.9 ^{ab} (15.2)	63.8 ^{ab} (5.8)	47.5 ^b (4.2)
Protozoa	107 (19.3)	52.8 (6.3)	42.9 (19.5)	46.6 (4.7)	27.3 (5.6)
Fungi : bacteria ratio	0.99 ^{ab} (0.05)	0.93 ^b (0.04)	0.74 ^c (0.04)	0.75 ^{abc} (0.06)	0.75 ^{ac} (0.01)
Gram+ : Gram– ratio	2.11 ^{ab} (0.13)	2.28 ^a (0.17)	2.06 ^{ab} (0.17)	1.96 ^{ab} (0.17)	1.53 ^b (0.14)

2010). Therefore, the dominance of saprophytic fungi may be associated with high acid phosphatase activity in the soils beneath *Dacrydium*. However, whether the greater acid phosphatase activity feeds back to the performance of seedlings underneath a *Dacrydium* canopy is not known.

SYNTHESIS

Our review of studies conducted on Mount Kinabalu suggests that podocarps regenerate successfully primarily under well-lit conditions like canopy gaps. Fast-growing angiosperm pioneers (e.g., *Macaranga* and *Ficus* species) generally outcompete podocarps under well-lit conditions in Bornean tropical rainforests. However, such fast-growing pioneer species generally have a greater demand for nutrients (particularly nitrogen) and thus are considered inefficient in photosynthetic nitrogen use. Such nutrient-demanding pioneer species cannot grow well on nutrient-limited soils. Furthermore, the montane zone appears to be too cool for angiosperm pioneers, whereas podocarps are well adapted to a wide thermal range.

Podocarps have a greater maximum tree size than most co-occurring angiosperm species. Once they reach

the upper canopy layer, they will persist for a long time because of their longer life span, which will allow them to regenerate in rare events of canopy gap formation that are unpredictable in both space and time. Where canopy structure is sparse because of poor tree growth on extremely infertile soils derived from ultramafic rocks, however, some conifer species seem to regenerate continuously.

Our studies also suggest that podocarps (*Dacrycarpus imbricatus* and *Dacrydium gracile*) in lower montane tropical rainforest may have a superior ability over co-occurring angiosperms in acquiring phosphate from organic forms of phosphorus. This ability is consistent with the dominance of podocarps on acidic Spodosols and soils derived from ultramafic rocks; in both cases labile phosphorus occurs primarily as organic phosphorus, and consequently, the dependence of trees (as well as soil microbes) on organic phosphorus increases. Because soil phosphorus is critical in these ecosystems (Spodosols and ultramafic soils), a slight difference in the ability to acquire soil phosphorus may explain the difference in photosynthetic ability and growth rate of podocarps compared to angiosperms. Angiosperms in these systems possibly cannot outcompete podocarps under conditions where phosphorus availability limits productivity.

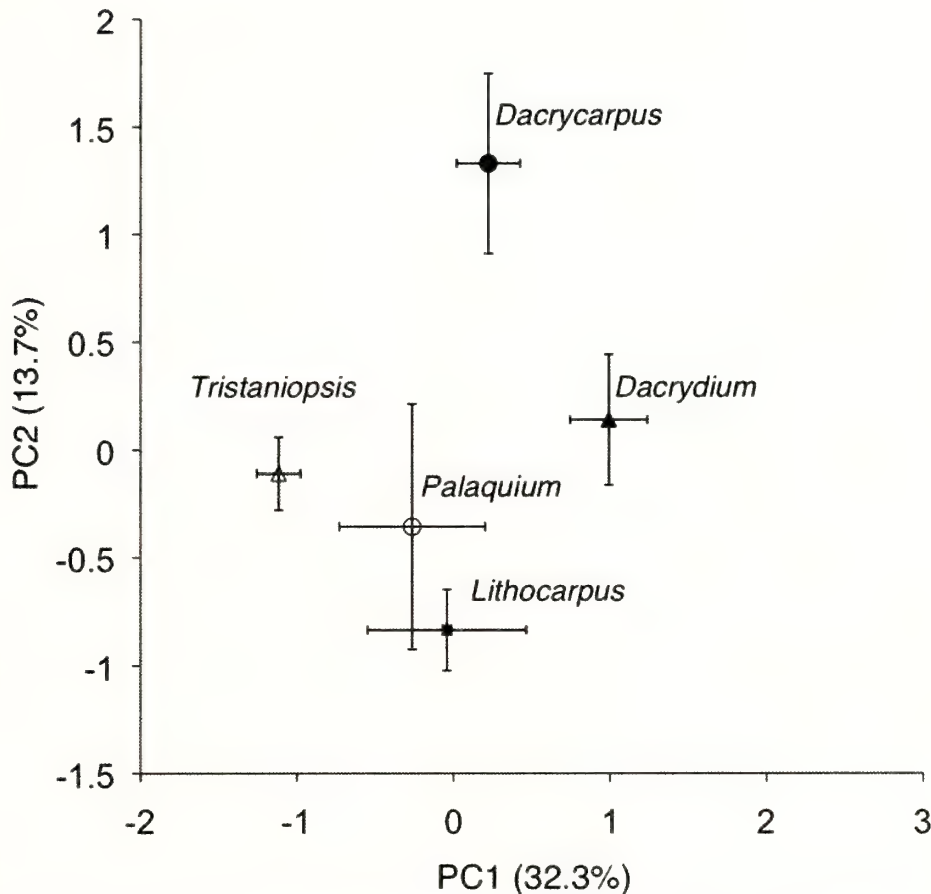


FIGURE 6.11. Principal components analysis (PCA) of soil lipids biomarkers. Lipid abundance was converted to mole percent values (each lipid abundance/total lipid abundance). The lipids with average mole percent < 0.5% were not included in the analysis. The mole percent values are not normally distributed, so the negative arcsine of the square root of each fatty acid mole percentage was used. Each point represents the mean of all soil samples for each species. *Dacrycarpus imbricatus* (solid circle) and *Dacrydium gracile* (solid triangle) are podocarps. *Lithocarpus clementianus* (solid square), *Palaquium rioense* (open circle), and *Tristaniopsis* sp. (open triangle) are angiosperms. Bars indicate the standard error of the mean and the percentages of variance explained by each axis are indicated in parentheses. Reproduced from Ushio et al. (2008).

However, phosphatase synthesis is a nitrogen-demanding process because phosphatase enzymes consist of proteins, yet we found no evidence that podocarps are superior in soil nitrogen acquisition to angiosperms. Kitayama et al. (1998, 2004) suggest that soil nitrogen mineralization is down-regulated by a decline in phosphorus availability in these systems, so soil microbes and soil nitrogen mineralization appear to be controlled by phosphorus availability. Therefore, the mechanisms of soil nitrogen acquisition must be resolved before the adaptation of podocarps to the nutrient-limited soils on Mount Kinabalu can be fully understood.

Finally, the phylogenetically associated genus *Agathis* (Araucariaceae) seems to share many traits with the podocarps. Comparison with *Agathis* would be useful to elucidate the unique ecological characteristics of podocarps in tropical forests.

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Temperate and Tropical Podocarps: How Ecologically Alike Are They?

*David A. Coomes and
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ABSTRACT. With few exceptions, podocarps are specialists of nutrient-poor soils within temperate and tropical rainforests. They are locally abundant in some tropical mountains, especially near the tree line, and in the lowland tropics most are confined to heathlands and impoverished habitats, although some can persist in forest understories. The ecology of tropical podocarps is not well understood, so here we draw on literature from temperate regions to help characterize their niches. Temperate podocarps are effective at capturing and retaining nutrients at the expense of competitors. They are universally slow growing, but this is not necessarily an encumbrance on poor soils because competition for light is relatively weak. Temperate podocarps are often outcompeted on richer soils because several factors stack against them: they are ill equipped to compete with angiosperms in the race to occupy canopy gaps, there may be few sites for their establishment on the forest floors, and continuous regeneration by podocarps is seldom found in the forest understory because their growth is severely hampered by shading. We suggest that competition excludes imbricate-leaved podocarps from most lowland tropical forests, whereas broad-leaved species with anastomosing veins (*Nageia* and some *Podocarpus*) are so shade tolerant that they regenerate beneath closed canopies.

INTRODUCTION

In 1989, Bond revisited an old but unresolved question: why were conifers pushed out of the lowland tropics and mesic temperate regions by angiosperms as they diversified and expanded in range during the Late Cretaceous? Previously, the leading hypothesis was that the evolution of flowers had given angiosperms overwhelming reproductive superiority over conifers: the wasteful process of wind pollination was usurped by directed pollination by animals (Raven, 1977). Bond (1989) and Midgley and Bond (1991) challenged the prevailing view, hypothesizing instead that the physiological traits of conifers made

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them inherently slow growing as seedlings. These traits place them at a competitive disadvantage during the regeneration phase of the life cycle but help them survive in extreme environments, including cold, droughts, nutrient-poor soils, poorly drained soils, and deep shade.

Two decades after Bond's "slow seedling" hypothesis, the latest physiological evidence indicates that podocarps are universally slow growing. Podocarps have long-lived leaves and low specific leaf areas, traits always associated with low photosynthetic capacity per unit leaf mass (Wright et al., 2004). They have lower photosynthetic capacity than angiosperms of comparable specific leaf area (Lusk, this volume). Using a global database of wood densities, we find that podocarps have denser wood than other conifers (Figure 7.1); this trait is associated with podocarps having narrower tracheids (Pittermann et al., 2006a; Lusk, this volume) and results in high hydraulic resistivity and low photosynthetic capacity per unit leaf area (Feild and Brodribb, 2001). In lowland cool temperate forests, diameter growth of podocarp trees is approximately half that of angiosperm trees under similar conditions (Ogden and Stewart, 1995; Bentley, 2007). In subalpine shrublands, podocarps grow more slowly than several angiosperms (P. Wardle, 1963a). Podocarps are slower growing than other commercially valuable timber species (Bergin, 2000). For example, *Podocarpus totara* seedlings with an initial mean height of 0.85 m reached just 2.9 m after 6 years and 5.5 m after 11 years in a provenance trial on fertile soils under frost-free conditions (Bergin et al., 2008), whereas *Pinus radiata* reaches heights up to 30 m after 17 years (Beets and Kimberley, 1993). Seedlings of *Lagarostrobos franklinii* in Tasmania grow at just 2.3 cm yr⁻¹, approximately a third of the rate of the angiosperm tree *Eucryphia milliganii*, which grows in nearby forests (Jennings et al., 2005). Podocarp seedlings are outpaced by angiosperms and even by tree ferns when growing on rich soils in southern New Zealand: height growth under optimal conditions is 3–7 cm yr⁻¹ versus 11–17 cm yr⁻¹ for subcanopy angiosperms and ~10 cm yr⁻¹ for tree ferns (Gaxiola et al., 2008; Coomes et al., 2009). We found no examples of fast-growing podocarps.

The notion that conifers are well equipped to cope with extreme environments remains unchallenged, but the mechanisms by which conifers are competitively disadvantaged in "productive" habitats are still a topic of debate. In the case of podocarps, there is considerable doubt over whether they can even be described as disadvantaged in lowland tropical habitats since a considerable number of shade-tolerant podocarps grow in the shade of tropical forests (e.g., Hill and Brodribb, 1999). The ~30 species of

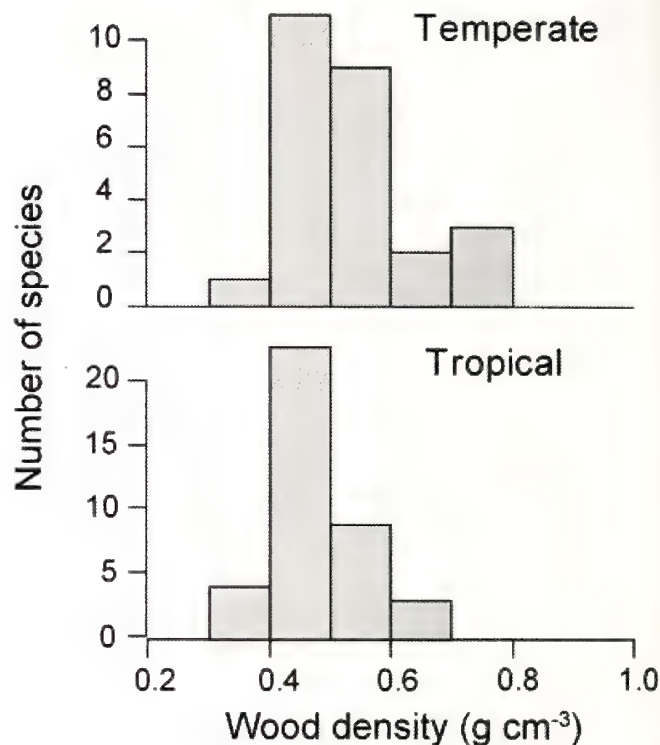


FIGURE 7.1. Wood density (oven-dry mass/fresh volume) of podocarp species from temperate and tropical regions (extracted from a global database; Chave et al., 2009). The Podocarpaceae have a greater mean wood density than six other conifer families (0.50 g cm^{-3} vs. mean of 0.45 g cm^{-3} ; $F_{7,260} = 9.7$, $P < 0.001$) and a similar mean density to the Taxaceae (0.53 g cm^{-3}). Tropical podocarps have a significantly lower wood density than their temperate relatives (0.48 ± 0.01 vs. $0.54 \pm 0.02 \text{ g cm}^{-3}$; $t = 2.1$, $P = 0.03$).

podocarps found in cool temperate forests have received much more attention from ecologists than the ~150 species of tropical and warm temperate forests. Can our understanding of the ecology of these temperate podocarps inform us about the distribution and dynamics of their tropical cousins? We start by discussing what types of habitats are occupied by temperate podocarps and why they are not observed in the full range of high-stress habitats occupied by conifers as a whole. We then explore the reasons why temperate podocarps often achieve dominance on nutrient-poor soils and why the exceptions prove the rule. We look at the regeneration strategies of temperate podocarps in shaded habitats and how these help explain the presence and persistence of some species in more nutrient-rich forests. These analyses lead us back to

a discussion of the ecology of tropical podocarps and why they are relatively uncommon in the lowlands.

LIMITS TO GEOGRAPHIC DISTRIBUTION: INTOLERANCE OF COLD AND DROUGHT

Podocarps prevail mostly in climates that are cool and wet. However, they do not tolerate extreme cold as well as Northern Hemisphere conifers: none can withstand temperatures below -20°C , whereas 88% of 117 Northern Hemisphere conifer species can do so (Figure 7.2; Bannister, 2007). Podocarps seldom form the tree line in temperate mountains but do so in tropical mountains. Instead, *Nothofagus* species often form tree lines in cool temperate South America, New Zealand, and Tasmania; podocarps are present but seldom form significant components of these forests (Wardle, 2008). Some temperate podocarps occur almost exclusively above tree lines as shrubs or prostrate woody plants in alpine ecosystems in New Zealand (Wardle, 1991) and Tasmania (Kirkpatrick, 1997). Perhaps differences in present and past climate have reduced the need and opportunity for the evolution

of traits conferring tolerance of extreme cold. Southern Hemisphere oceans act as vast heat buffers that moderate land temperatures, resulting in milder climates than in the Northern Hemisphere. The Southern Hemisphere was also less extensively glaciated during the Pleistocene (Sakai et al., 1981). Mild climates throughout much of the evolutionary history of the Southern Hemisphere may be responsible for its paucity of cold-tolerant trees: New Zealand's tree lines, at 1,200–1,300 m, are about 500 m lower than continental tree lines at equivalent continental latitudes (Körner and Paulsen, 2004).

Although podocarps are ill equipped to survive in extreme cold, they are relatively well protected against moderate frosts experienced in their current ranges. Frosts in New Zealand's North Island damage the dominant shade-tolerant angiosperm (*Beilschmiedia tawa*) but have no apparent effect on co-occurring podocarps (Kelly, 1987). Pot-grown podocarp seedlings are more tolerant of sub-zero temperatures than angiosperms taken from the same region (Bannister and Lord, 2006). Hardiness of *Podocarpus totara* in New Zealand has a strong genetic basis, with genotypes from the coldest regions being most hardy, suggesting that populations have evolved in response to

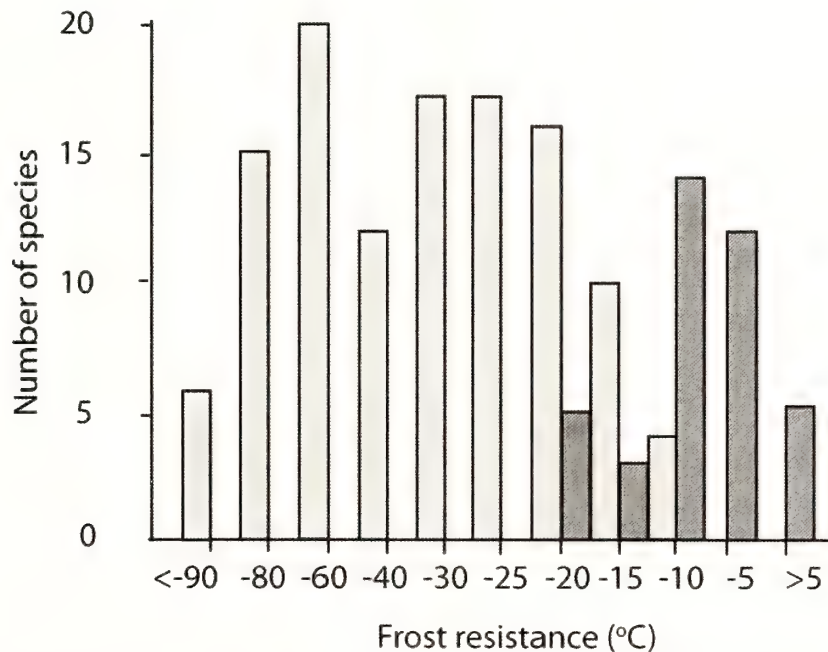


FIGURE 7.2. Frost resistance of conifers from the Northern (light gray) and Southern (dark gray) hemispheres, redrawn from Bannister (2007). Frost resistance was quantified by calculating the temperature at which half of the leaves are damaged by the effects of cold.

environmental pressures (Hawkins et al., 1991). Their frost hardiness appears to come at a cost, in that maximum growth rates of high-latitude genotypes are slower (Bergin et al., 2008). Angiosperms in Tasmanian montane heaths suffer much greater loss in xylem conductivity after being frozen and thawed (17%–83%) than do conifers (<12%), primarily, it seems, because bubbles in the xylem conduits formed during the freeze-thaw cycle are more easily redissolved in the narrow tracheids of conifers than in the wider vessels of angiosperms (Feild and Brodribb, 2001).

Few temperate podocarps grow in dry regions, in contrast to other conifers, and this intolerance can be traced to their vascular systems (see also Brodribb, this volume). Exceptions include *Afrocarpus falcatus* in drier regions of southern Africa (Adie and Lawes, this volume), *Podocarpus drouynianus* in Western Australia (Ladd and Enright, this volume), and *Halocarpus bidwillii*, *Phyllocladus alpinus*, and *Podocarpus hallii* in the dry lowland forests of New Zealand (~400 mm yr⁻¹; Bergin, 2000; McGlone, 2001). Drought damages plants if the tension within water columns of the vascular system gets so large (i.e., the water potential gets so low) that cavitation occurs or if conduits implode (Tyree and Sperry, 1989). Plants from dry regions, such as conifers in the Pinaceae and Cupressaceae, withstand high tensions within their vascular systems by having thick tracheid walls that prevent implosion and “plugs” (torus margo) within pit membranes that prevent air bubbles from moving through the vascular system (Pittermann et al., 2006b). However, podocarps are peculiar among conifers in being susceptible to embolism at relatively low tensions, despite having thick tracheid walls (Pittermann et al., 2006b) and having relatively high hydraulic resistance across pit membranes (Pittermann et al., 2006a). It may also be the case that sclereids in podocarp leaves are vulnerable to implosion under tension (Brodribb, this volume). Plants can avoid damage by early closure of stomata, but we found no studies of stomatal responses in podocarps. Podocarps have long-lived leaves, so they are unable to drop all their leaves during dry periods in the way that many drought-deciduous angiosperms do. In one example, *Podocarpus totara* lost many leaves during a drought year, produced shorter leaves, and maintained high internal water potential but fared less well than drought-tolerant angiosperms (Innes and Kelly, 1992).

TOLERANCE OF NUTRIENT-POOR SOILS

With a few important exceptions, podocarps in the cool temperate regions achieve greatest abundance on the

poorer soils and/or in open habitats. In the coastal range of Chile, two podocarps are most common on shallow mica schists and poorly drained sites (Lusk, 1996), and *Lepidothamnus fonkii* has a dwarf habit and grows in *Sphagnum* bogs (Gardner et al., 2006). In Japan, *Nageia nagi* occurs on thin soils derived from granite on Yakushima (Kohyama and Grubb, 1994), but it is not restricted to poor soils. In southeastern Australia, *Podocarpus lawrencei* occurs on acidic soils on granite and weathered sedimentary rocks, achieving greatest abundance on skeletal soils (Barker, 1991). In New Zealand, podocarps often achieve greatest abundance on poor soils, as shown by investigations on two soil chronosequences: a series of deglaciated terraces near the Franz Josef Glacier and a series of uplifted marine terraces in southern Fiordland. On both chronosequences, plant-available phosphorus becomes depleted on the older sites, and podocarps become increasingly abundant on these impoverished soils, with some species restricted to them (Richardson et al., 2004; Coomes et al., 2005). Bond (1989) proposed that conifers are successful on poor soils because they are almost unrivalled in their tolerance of extreme environments and because competition for resources is neither intense nor important; conifers are stereotyped as “stress tolerators” in the competitor–stress tolerator–ruderal triangle of Grime (1977). Here we argue that podocarps possess traits that allow them not only to tolerate poor soils but also to be successful competitors for belowground resources.

EFFICIENT CAPTURE OF NUTRIENTS

Fungal hyphae have high area to mass ratios, making them more efficient than roots at foraging for immobile nutrients. Podocarps rely heavily on endomycorrhizal symbionts for nutrient uptake (Baylis, 1969; Russell et al., 2002). Fine roots have low specific root length (Gaxiola et al., 2010) and are heavily infected by mycorrhizal fungi (up to nearly 100% of root length; Dickie and Holdaway, this volume). Podocarps on the Franz Josef chronosequence had lower foliar nitrogen to phosphorus ratios than ferns or angiosperms on the phosphorus-impoverished soils, suggesting that they were better able to extract soil phosphorus (Richardson et al., 2005). Angiosperm species from podocarp-rich forests are also heavily infected by arbuscular mycorrhizas (Hurst et al., 2002), but very little is known about the comparative efficiency of these groups. Slow-growing conifers from the Northern Hemisphere allocate a large proportion of their net primary productivity to roots and ectomycorrhizal fungi, particularly when nutrients are in short supply (Hobbie, 2006). The same may

be true of podocarps: Whitehead et al. (2004) concluded that *Dacrydium cupressinum* in New Zealand swamp forests allocate a high proportion of total carbon below-ground, on the basis of the predictions of a process-based simulation model. New Zealand podocarp seedlings have a higher root to shoot ratio than many angiosperm trees, particularly when grown in nutrient-poor soils.

INCREASED NUTRIENT RETENTION OF LONG-LIVED LEAVES

Species associated with nutrient-poor soils often have long-lived leaves (Grime, 1977; Chapin, 1980; McGlone et al., 2004) because a long life span reduces the annual rate of mineral nutrient loss via abscission (Monk, 1966). Plants salvage only about 50% of nitrogen and 60% of phosphorus from leaves during abscission (although there is great variability among species), so retaining leaves is strongly advantageous in situations where recapturing nutrients is costly (Aerts, 1995). Podocarp leaves have long life spans compared with angiosperm associates; Gaxiola (2006) observed that four podocarps species from the Waitutu chronosequence in southern New Zealand had a mean leaf life span of 3.1 years, compared with 1.5 years for 11 angiosperm species (nine of which were evergreen). Lusk (2001) measured leaf life spans of several Chilean species, including the following podocarps: *Podocarpus nubigenus* (7.3 years), *Podocarpus salignus* (3.2 years), and *Saxegothaea conspicua* (4.2 years). Podocarp leaves contain significant quantities of terpenes (Brophy et al., 2000), which are known to deter herbivores. However, whether podocarps are better defended than angiosperm is difficult to judge objectively because terpenes are just one of the armory of defenses that plants deploy.

LONGEVITY AND NUTRIENT RETENTION

Some temperate conifers, including podocarps, have much longer life spans than co-occurring angiosperm trees (Wardle, 1991; Enright and Ogden, 1995). This is especially the case for some New Zealand podocarps (Lusk and Ogden, 1992; Bentley, 2007) and *Lagarostrobos franklinii* in Tasmania (Gibson and Brown, 1991). However, great longevity is not a feature of podocarps, whereas it is of other conifers in the same forests (e.g., *Cryptomeria japonica* and *Tsuga sieboldii* in Japan, *Fitzroya cupressoides* in Chile, and *Picea balfouriana* in China). A tree releases nutrients back to the soil upon its death, so a long life span is advantageous in situations where regaining those nutrients requires intense competition with neighbors (Ogden and Stewart, 1995; Coomes et al., 2005). A long life span

requires wood that is strong and resistant to boring insects and rot. Podocarps have denser wood than other conifers (Figure 7.1), indicating that the wood is likely to be mechanically strong (Chave et al., 2009). Many podocarp species are prized for their timbers because they are resistant to rot, and powerful antimicrobial chemicals have been isolated from the bark of several *Podocarpus* species (Abdillahi et al., 2008). An array of diterpenoids within bark (Cox et al., 2007), as well as the deposition of phenolics in specialized parenchyma cells (Hudgins et al., 2004), provides robust defense against insects.

ECOSYSTEM ENGINEERS THAT STARVE NEIGHBORS OF NUTRIENTS

The tough fibrous leaves of New Zealand's podocarps are slow to decompose (Wardle et al., 2008; Hoorens et al., 2010), resulting in the accumulation of organic matter within soils, an increase in the ratios of carbon to phosphorus and nitrogen to phosphorus in soil, and effects on community structure of soil microflora (Wardle et al., 2008). Nutrients are sequestered within the recalcitrant organic matter. Locking up nutrients in this way is an effective means of competing for nutrients if competitors are relatively intolerant of extreme nutrient shortage or less able to access organic nutrients. In effect, podocarps may engineer their local environment to their own advantage.

TOLERATORS OF SOIL ANOXIA

Nutrient-poor soils in high rainfall regions are often poorly drained as a result of subsoil cementation. Species that tolerate low concentrations of soil oxygen and mobilization of toxic ions are advantaged under these conditions. A pot experiment with three New Zealand podocarps showed them to survive well, with much reduced growth, under waterlogged conditions (Gaxiola et al., 2010). The prevalence of conifers in waterlogged sites, both in New Zealand and in other temperate forests, appears to result from various morphological and biochemical adaptations (Crawford, 1987). One New Zealand podocarp, *Manoao colensoi*, produces aerenchyma in its roots that carries air down to submerged fine roots (Molloy, 1995), but no other examples of this in podocarps are known. The reduced stature of podocarps associated with bogs (e.g., *Lepidothamnus intermedius* and *Halocarpus biformis* in New Zealand) may result from a lack of deep anchoring roots in anoxic soils, without which woody plants are unable to grow tall (Crawford et al., 2003).

REDUCED IMPACT FROM ASYMMETRIC
COMPETITION FOR LIGHT

Podocarps are slow growing, which is not necessarily disadvantageous on poor soils, where resource limitations reduce the potential for fast growth regardless of a species' genetic potential. Forests on nutrient poor and waterlogged soils often have comparatively low leaf area indices and intercept less light (Coomes and Grubb, 2000). For example, 1.5% of incoming photosynthetically active radiation makes its way to the forest floor of phosphorus-rich soils in southern New Zealand, 4.6% gets through on phosphorus-depleted soils, and 16% gets through on even poorer sites (Coomes et al., 2005). The growth of podocarps is hardly influenced by competition from taller neighbors on the poor soils (e.g., Figure 7.3a). As long as competition for light is not intense, podocarps may exclude other plants from nutrient-poor soils through belowground competition (see Coomes and Grubb, 2000).

CANOPY ARCHITECTURE SUITED TO
GROWTH IN THE OPEN

Genera of podocarps associated with poor soils often have small, scalelike leaves held on upright or pendent stems (*Dacrydium*, *Halocarpus*, *Lepidothamnus*, *Manoao*, *Microcachrys*, and *Microstrobos*) or have whorls of leaves that overlap. Steeply inclined or clustered leaves reduce light interception at the top of the canopy, allowing light to "trickle down" to lower leaves. This increases whole-plant photosynthesis because the uppermost leaves receive near-optimal rather than excessive light levels, while leaves at the bottom of the canopy get a greater share of resources (Horn, 1971). The world's fastest-growing trees (*Betula*, *Casuarina*, and some *Pinus* and *Eucalyptus*) have this canopy architecture, at least once past the seedling stage. However, clumped and pendent leaves are inefficient at scavenging light in deeply shaded understories and ineffective when competing for light against fast-growing neighbors (Leverenz et al.,

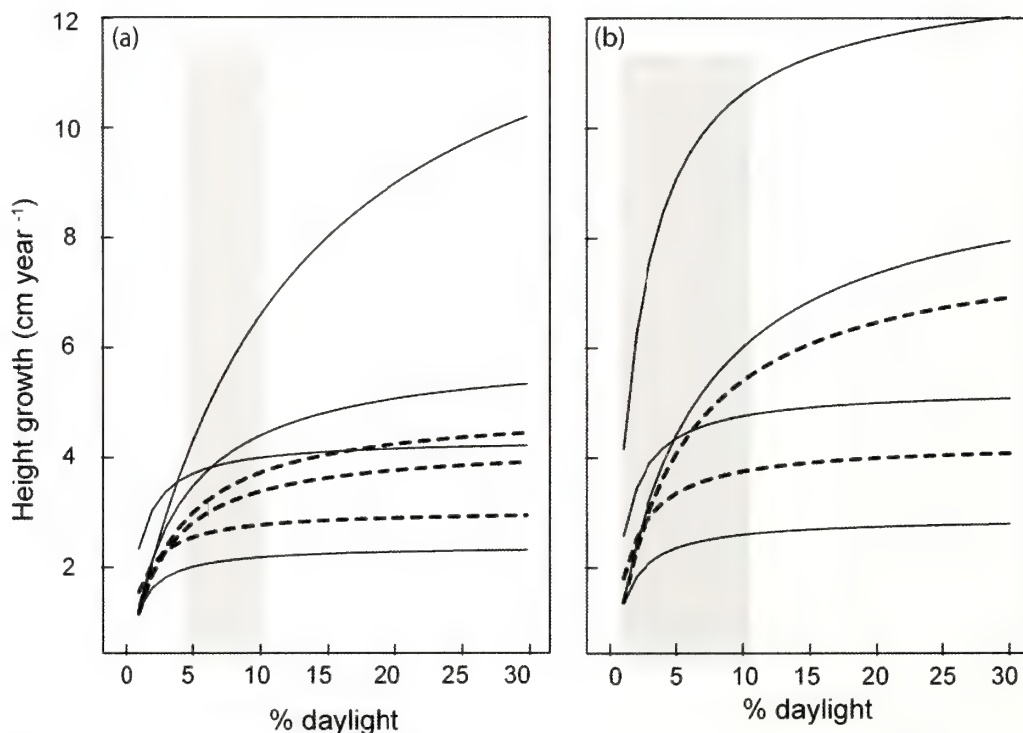


FIGURE 7.3. Height growth of podocarp (dashed line) and angiosperm (solid line) tree seedlings in response to light on (a) phosphorus-depleted terraces versus (b) alluvial terraces in southern New Zealand. The gray bars indicate the percentage daylight typically found at 1.35 m above ground under the canopy, based on the 20th and 80th percentiles of light measurements (redrawn from Coomes et al., 2009).

2000; Pickup et al., 2005). Therefore, these architectures are uncommon in infrequently disturbed communities growing on nutrient-rich soils where competition for light is intense (Horn, 1971).

EFFICIENT USE OF LIGHT

The efficient use of whole-canopy light has been investigated in detail for *Dacrydium cupressinum*, which has scalelike leaves positioned on pendent shoots; closed stands have a leaf area index of only 2.0 m² m⁻² and intercept only 79% of available photosynthetically active radiation when growing on acidic, poorly drained soil (Whitehead et al., 2002). Clumping of leaves within the canopy of *Dacrydium*-dominated forest reduces canopy light interception by 5% but increases canopy photosynthesis by 8% through increased light use efficiency (Walcroft et al., 2005). Even though leaves in the upper crown of *Dacrydium* on poor soils have a maximum rate of carboxylation activity (half-surface leaf area basis) that is only 24% of that of similarly positioned leaves within an oak woodland on nitrogen-enriched soils in summer, the annual carbon uptake rate of the podocarp forest was only 14% lower than that of oak because of its canopy organization (Whitehead et al., 2004). The canopy architecture and evergreen leaves, which continued to take up carbon in winter, contributed to a higher-than-expected carbon uptake rate.

SUMMARY

Podocarps are successful on poor soils because they are well adapted to acquiring and retaining nutrients. It may be that podocarps function similarly to slow-growing conifers from the Northern Hemisphere, allocating a large percentage of net primary productivity belowground and thereby enabling their roots systems (and associated mycorrhizas) to forage exhaustively for soil nutrients. In addition, their long-lived leaves, durable wood, and slowly decomposing litter ensure that hard-earned nutrients are not relinquished to competitors. Inherently slow stem growth may not be a serious encumbrance when nutrients are in short supply because asymmetric competition for light is weak, so outgrowing neighbors is not strongly advantageous. Any disadvantages that accrue from slow growth are offset by effective nutrient recovery and retention, longevity, and strength to resist catastrophic disturbance. Scalelike leaves are advantageous in terms of whole-plant photosynthesis in open habitats.

REGENERATION PROCESSES

RESPONSES TO FOREST DISTURBANCE

Much attention has been given to the role of disturbances in allowing species with differing regeneration niches to coexist within forests (Poorter and Bongers, 2006). In the context of Southern Hemisphere conifers, Ogden and Stewart (1995) recognized three categories of regeneration response to disturbance: (1) "Catastrophic regeneration" occurs in the aftermath of infrequent massive disturbances (e.g., earthquakes, floods, fires, and cyclones) and is characterized by a pulse of establishment after which no further establishment is possible; at the landscape scale, catastrophic regeneration gives rise to large patches (>1,000 m²) of similarly aged trees and strong discontinuities in age structure within and among patches. (2) "Gap-phase regeneration" occurs in smaller gaps (<1,000 m²) created by the death a single tree or a few trees; it is characterized by smaller patches and fewer discontinuities in age. (3) "Continuous regeneration" occurs when seedlings and saplings are capable of growing and surviving in the shade of an intact canopy. Typically, these shade-tolerant trees edge slowly upward in the shade, growing more quickly if openings appear in the canopy above them (e.g., Uhl et al., 1988); near-continuous regeneration gives rise to all-aged population structures, composed of many small stems and successively fewer stem in larger age classes.

Temperate podocarps vary greatly in shade tolerance. Some have developed flattened leaves arranged within planes, a shade adaptation that may have arisen in response to changes in light transmissions brought about by the evolution of shade-bearing angiosperms in the early Cenozoic (Hill and Brodribb, 1999; Brodribb and Hill, 2003a, 2003b). Podocarps with shade-tolerant leaf morphology also have shade-tolerant physiology (Brodribb, this volume) and are sometimes capable of continuous regeneration. For example, *Nageia nagi* has large, flattened leaves and regenerates nearly continuously within Japanese warm temperate rainforests (Kohyama, 1986), and *Prumnopitys ferruginea* has shade-tolerant morphology and is quite capable of establishing without multiple-tree gaps in New Zealand (Figure 7.4; Duncan, 1993; Lusk and Smith, 1998; Bentley, 2007). Other species have tiny, scalelike leaves held on upright stems and are unable to tolerate prolonged shade: when adult, *Halocarpus biformis*, a small tree with imbricate scale leaves, is most frequent in open habitats, such as the margins of bogs (Figure 7.4).

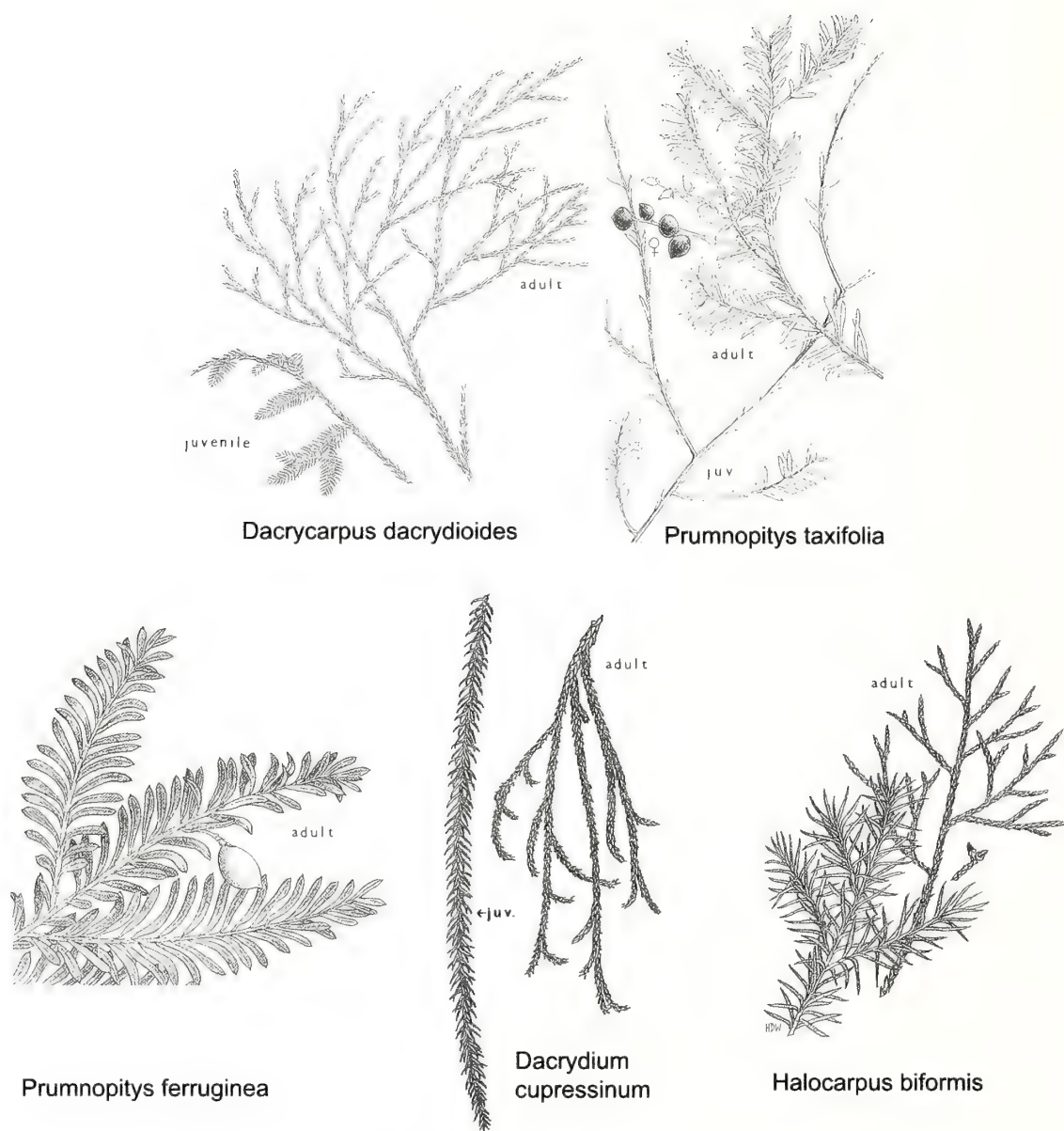


FIGURE 7.4. Juvenile and adult foliage of contrasting podocarps from New Zealand. Drawings modified from Wilson (1982) and reproduced with kind permission of the author and publisher.

REGENERATION PROCESSES IN RELATION TO SOIL FERTILITY

Regeneration response depends not only on a species' inherent shade tolerance but also on the light conditions in the understory of the forest. A species capable of regenerating continuously under open forests on poor soils may struggle to regenerate under dense forests on richer soils. For example, two podocarps that grow in the

Chilean coastal range, *Podocarpus nubigenus* and *Saxegothaea conspicua*, are considered the most shade tolerant of all conifers in temperate South America (Donoso, 1989). They attain greatest abundance on shallow soils (poorly drained sites in the lowlands, ridges, and shallow mica schist at higher altitudes). The main angiosperms at these sites (*Nothofagus nitida* and *Weinmannia trichosperma*) have open canopies under which the podocarps regenerate: there are many seedlings and saplings in the

forest understory, and the tree populations have reverse-J age distributions (Lusk, 1996; Gutiérrez et al., 2004). However, at sites where shade-casting angiosperms such as *Dasyphyllum diacanthoides* and *Laureliopsis philippiana* are common, the podocarps are less abundant and regeneration discontinuous (Lusk, 1996). At sites where shade-tolerant angiosperms are dominant, the podocarps are excluded altogether (e.g., Armesto and Fuentes, 1988). In Tasmania, *Lagarostrobos franklinii* appears to regenerate along rivers that frequently flood but rarely penetrates into closed rainforest (Gibson and Brown, 1991). In South Africa, *Podocarpus latifolius* grows and survives well in the understory of angiosperm-dominated warm temperate forest in the Drakensberg Mountains (5.5% light transmission to forest floor; Adie and Lawes, 2009a) but is unable to regenerate beneath coastal subtropical forest in KwaZulu-Natal, through which only ~1% light is transmitted (Adie and Lawes, 2009b). However, the regeneration success of *P. latifolius* is not simply determined by competition for light: seedlings are unable to establish under mature podocarp forest, even though 7.5% light penetrates to the forest floor, apparently because grasses and/or mature trees exclude seedlings by belowground competition (Adie and Lawes, 2009a). Various other studies indicate that that temperate podocarps fail to regenerate beneath parent trees (e.g., Norton, 1991; Cameron, 1960; Ogden and Stewart, 1995).

WHY SHADE-TOLERANT PODOCARPS FAIL TO REGENERATE IN THE SHADE

Many podocarps persist in deep shade (e.g., mortality rates in New Zealand lowland forest were just 1% per year; Smale and Kimberley, 1986), but survival counts for little unless accompanied by height growth. Height growth of New Zealand podocarps is strongly suppressed by shading (e.g., Smale and Kimberley, 1986; Ebbett and Ogden, 1998; Coomes et al., 2009; Figure 7.3), limiting opportunities for continuous regeneration in forest understories. For instance, *Podocarpus hallii* seedlings in a cool montane rainforest in New Zealand have an annual mortality rate of just 2.7%, meaning that about 5% of seedlings live for at least 100 years, but height growth is so slow that virtually no individuals get past the seedling stage in the shade; consequently, most regeneration is restricted to landslides (Bellingham and Richardson, 2006). Similarly, *Dacrydium cupressinum* seedlings had an annual mortality rate of 10% and a height growth of 1.5–2.5 cm yr⁻¹ in a lowland New Zealand forest on highly leached soils, indicating that height growth is insufficient

for seedlings to regenerate continuously in these forests (Coomes et al., 2009; Kunstler et al., 2009). Instead, *Dacrydium cupressinum* requires progressive overstory mortality (Six Dijkstra et al., 1985; Lusk and Ogden, 1992; Lusk and Smith, 1998; Bentley, 2007) or catastrophic disturbance (e.g., Duncan, 1993; Smale et al., 1997) in order to regenerate. Even highly shade-tolerant podocarps such as *Prumnopitys ferruginea* can struggle to get beyond the seedling stage in lowland forests (Smale et al., 1997), and stands of this species have a discontinuous age structure at some sites (e.g., Lusk and Ogden, 1992). The important implication is that shade tolerance assessed from leaf physiology does not necessarily equate with ability to regenerate continuously within a particular habitat. The latter depends upon the degree of shade cast by the forest as well as the physiological shade tolerance of the species and is affected by changes in shade tolerance with size (Kunstler et al., 2009).

RELiance ON CATASTROPHIC DISTURBANCE IN NUTRIENT-RICH HABITATS

Three species of podocarps dominate the alluvial floodplain forests of New Zealand, apparently contradicting the theory that podocarps are competitively excluded from nutrient-rich sites. *Dacrycarpus dacrydioides* is a dominant tree on poorly drained soils (Smale, 1984; Duncan, 1993; Norton, 1995), and *Prumnopitys taxifolia* and *Podocarpus totara* are dominant on better-drained soils (Esler, 1978; McSweeney, 1982). Establishment opportunities can be limited by near-continuous fern cover at some sites (Coomes et al., 2005), and although smaller-seeded angiosperms are able to take advantage of elevated sites such as fallen trunks and tree fern stems, the larger-seeded podocarps seldom establish in such niches (Lusk, 1995; Christie and Armesto, 2003; Lusk and Kelly, 2003; Gaxiola et al., 2008). Indeed, none of these podocarps can regenerate continuously beneath mature rainforest canopies (e.g., Ulrich et al., 2005). Neither is gap-phase regeneration possible because tree fall gaps are colonized rapidly by fast-growing woody angiosperms, ferns, and herbaceous plants, leaving few opportunities for slow-growing trees (Coomes et al., 2005, 2009). Instead, slow-growing podocarps are able to persist in the floodplain forests in western South Island rainforests by regenerating after catastrophic disturbances, such as those resulting from debris triggered by major movements of faults in the Southern Alps and associated floods (Wells et al., 2001; Cullen et al., 2003). The long life span of these podocarps allows them to persist from one rare catastrophic disturbance to

the next (Enright and Ogden, 1995; Veblen et al., 1995; Lusk and Smith, 1998). Currently, regeneration failure and ageing populations are observed over most of their range (Holloway, 1954; Wardle, 1963b), and in some regions this could be because the last major movement of the Alpine fault was nearly 300 years ago (AD 1717; Wells et al., 1999). An event every few hundred years is sufficient to maintain conifers as dominant elements (i.e., a "storage effect" sensu Chesson, 2000). However, catastrophic regeneration of podocarps may be uncommon outside New Zealand. Other species, such as the two Japanese species in typhoon-affected forests, may benefit from disturbance events by being relatively resistant to damage (see Dalling et al., this volume).

Floodplain podocarps grow well in bare mineral soil (e.g., Wardle, 1974) and presumably benefit from reduced competition with angiosperms on fresh alluvium. However, they are not pioneer species, as they arrive after an initial wave of colonization by early successional plants (e.g., Reif and Allen, 1988). Woody plants such as *Aristotelia serrata* and *Melicytus ramiflorus* grow quickly and form an open canopy; birds feed on the pseudo-arils of podocarps and disperse the seeds into these early successional communities (Beveridge, 1964; Wardle, 1991). The podocarps grow up beneath the open-crowned bushes and trees and eventually overtop them (Beveridge, 1973), continuing to colonize sites for many decades after disturbance (e.g., Wells et al., 2001). Interestingly, *Dacrycarpus dacrydioides* and *Prumnopitys taxifolia* undergo a major switch in leaf morphology at this stage, from having relatively broad leaves held in planes to having small leaves on pendant branches (Atkinson and Greenwood, 1989). These changes may be responses to increased light and exposure once the trees have overtopped the early successional community (McGlone and Webb, 1981). New Zealand has a disproportionate number of long-lived podocarps that rely on flooding, although they are also represented in Tasmania and mainland Australia (Barker, 1991; Gibson and Brown, 1991).

INTOLERANCE OF FIRE

Fire disturbance is usually fatal for podocarps, although two Australian podocarps (*Podocarpus drouynianus* and *P. spinulosus*) resist fire by sprouting from belowground reserves (Chalwell and Ladd, 2005; Ladd and Enright, this volume) and *Halocarpus bidwillii* can regenerate after fire in New Zealand heathlands (Wardle, 1991). The increased frequency of fire since the arrival of humans is thought to be the major factor of range contraction of podocarps in Australia (Hill and Brodribb, 1999),

and it all but annihilated forests formerly dominated by podocarps in eastern New Zealand (McGlone, 2001). Podocarps lack traits found in fire-adapted coniferous lineages, such as serotinous cones, an ability to resprout from the roots, and highly flammable leaves and litter. Several *Podocarpus* species have thin bark, suggesting that their vascular cambium could be susceptible to damage during fire. Highly flammable myrtaceous shrubs are the early colonizers of burnt areas in the North Island of New Zealand; the shrublands are soon colonized by podocarps, but fire must be excluded for several decades in order for the trees to overtop the shrubland and form a dense forest (McKelvey, 1963; Ogden and Stewart, 1995; Wilmschurst and McGlone, 1996).

RESPROUTING

Tall podocarp species do not, in general, resprout following damage (Martin and Ogden, 2006). For example, in New Zealand forests there was no resprouting of *Dacrydium cupressinum* after logging, and regeneration was dominated by resprouts of the angiosperm tree *Weinmannia racemosa*, to the disadvantage of *D. cupressinum* (Baxter and Norton, 1989). Saplings of *D. cupressinum* were unable to recover after experimental clipping to simulate deer browse because they resprouted poorly (Bee et al., 2007). Typhoon-damaged trees of the podocarp *Nageia nagi* in southern Japan were also ineffective at resprouting, in contrast to many co-occurring angiosperm trees (Bellingham et al., 1996). Resprouting is more apparent for temperate podocarps from poor sites, which are often shrubs or small trees and exhibit multitemmed architecture. These include *Halocarpus bidwillii*, *Lepidothamnus intermedius*, and *Lagarostrobos franklinii*, all of which spread vegetatively in open habitats. By doing so, patches of *L. franklinii* may have persisted for 10,000 years, and trees within remnant populations are genetically homogenous (Clark and Carbone, 2008). Another tree of open habitats, *Phyllocladus alpinus*, resprouts after wind damage (Martin and Ogden, 2006). A taller podocarp in Chilean rainforests, *Saxegothaea conspicua*, exhibits vegetative regeneration, which is crucial for its maintenance under shade-tolerant angiosperms in undisturbed stands (Veblen et al., 1980; Lusk, 1996).

SUMMARY

Podocarps are ill equipped to compete with angiosperms in the race for light in canopy gaps. Some species have evolved to tolerate prolonged shade, and these may regenerate continuously under relatively open-canopied

forest on poorer soils. However, few species can regenerate continuously under forests that are rich in shade-tolerant trees, tree ferns, bamboos, or ground plants because establishment sites are limited in these forests and onward growth is severely hampered. In New Zealand, three podocarp species dominate forests on rich alluvial soils—they do this by escaping competitors when fresh mineral surfaces are created by catastrophic disturbance events. These events may occur every few hundred years, and the long life spans of conifers allow them to persist from one event to the next.

ECOLOGY OF TROPICAL PODOCARPS

The biogeography of tropical podocarps is dealt with in other chapters but can be summarized as follows: podocarps are dominant elements of forests on a variety of soils in the mountains of Papua New Guinea, Southeast Asia, and subtropical and tropical Africa but are not dominant in the mountains of northern Australia, New Caledonia, and Madagascar and are only locally dominant in South America. There are a few lowland species in Australasia, the Pacific Islands, India, Africa, and the Americas; these can dominate poor soils but are rare in other lowland forest types (P. J. Grubb, University of Cambridge, personal communication; Wade and McVean, 1969; Enright, 1995).

TOLERANCE OF COLD AND HEAT

Tropical podocarps differ from those in temperate regions in being a major alpine element of tree lines over a wide area (e.g., New Guinea; Grubb and Stevens, 1985), indicating that they are among the least warmth-demanding trees in the tropics. They are also among the most tolerant, forming dense, almost pure stands immediately around frost hollow grassland (Grubb and Stevens, 1985). Like most temperate podocarps, they are excluded from dry regions: although *Afrocarpus falcatus* is common in relatively dry forests of Africa, the overwhelming majority of species are restricted to the wet tropics. Podocarps have easily distinguishable pollen, and the observation that tropical podocarps prevail mostly in climates that are cool and wet is frequently used by palynologists to reconstruct paleoclimates. Thus, the spread of podocarps into lowland Amazonia during Pleistocene glaciations suggests cooler conditions in the basin (Colinvaux et al., 1996), whereas the upward migration of podocarps into the páramo grasslands suggests a period of warmer climate in the Peruvian Andes between 8900 and 3300 BP. As a further example, the waxing and waning

of podocarp-rich rainforests across southeastern Australia during the late Pliocene and Pleistocene (Brodrribb and Hill, 2003b; Sniderman et al., 2007) and the Late Cretaceous (Gallagher et al., 2008) is interpreted in terms of shifts in rainfall patterns driven by Milankovitch cycles (greater summer insolation resulting in warmer tropical seas, bringing greater rainfall to the continent).

SUCCESS ON POOR SOILS

Many tropical podocarps are restricted to poor soils. In the appendix we provide brief descriptions of 96 species of tropical, subtropical, and warm temperate podocarps, taken mostly from Earle (1997–2009). We categorized each species as either (1) restricted to outstandingly poor soils, (2) restricted to rich soils, or (3) found on both rich and poor soils. “Outstandingly poor soils” included ultramafic soils, podzolized sands, peats, and shallow soils associated with limestone, sandstone, coastal bluffs, and ridgetops. We also included species associated with tree lines in the outstandingly poor soils category, the soils being highly organic and probably with markedly low rates of nitrogen mineralization (P. J. Grubb, pers. comm.). We subdivided their habitats into montane and lowland rainforest species (montane is defined here as >1,000 m elevation in the tropics and >800 m in the subtropics and warm temperate regions).

Most tropical podocarps in Earle’s database are found in mountains (56%), so the majority of the species occupy cool climates. Several of these species (21) are described as locally common, dominant, or forming pure stands at high altitude, on ridges and sometimes in peats. They include *Dacrycarpus* (3), *Dacrydium* (7), and *Podocarpus* (9). Half of the montane species are also found in “normal” montane forests as well as on poor soils, but they are often less common when off the poorest soils: this group includes all seven species of *Dacrycarpus*. Nine species appear to be restricted to “normal” montane forests (i.e., they are not mentioned as growing on poor soils in their ecological descriptions).

In the lowlands, 11 species are restricted to extremely poor soils, 12 are common on poor soils but venture into forest on better soils, and 9 are found in “typical” lowland rainforest. The last group comprises three genera: *Nageia* (3), *Podocarpus* (5), and *Parasitaxus* (1). The *Nageia* species are shade-tolerant trees of warm temperate and subtropical forests (Kohyama, 1986) and are canopy species that are “scattered” and “often common” in the forest understory. The *Podocarpus* species are described as “scattered” and “locally common,” and all are subcanopy (~25 m tall), except *P. spinulosus*, which is a shrub restricted to sheltered coastal sites and gullies. Finally, *Parasitaxus usta* (New

Caledonia) is the only parasitic gymnosperm and never grows taller than 2 m; it persists in shade by virtue of the carbon it gains by parasitism on the roots of *Falcatifolium taxoides*. The 11 species restricted to poor soils are found on peat swamps, kerangas, and ultramafics; they include *Dacrydium* (3), *Falcatifolium* (2), and *Podocarpus* (6). Six of these species are small trees (<12 m tall).

Presumably, podocarps are successful on the poorest tropical soils for the same reasons as in temperate regions. The species restricted to the poorest soils are significantly shorter and have much smaller leaves than species of better soils (e.g., Aiba and Kitayama, 1999), with species associated with both soil types having intermediate height and leaf area (Table 7.1; significance based on analysis of variance). These patterns are observed in both lowland and montane forests. The trend is precisely as anticipated, given that asymmetric competition for light is less intense among plants growing on poor soils, so height growth is not as strongly advantageous, and small leaves held on upright stems are effective for whole-plant photosynthesis within open forest. In lowland and lower montane forests, the heights achieved by podocarps are unremarkable, but at high altitude the species are often emergent. The area of shade leaves (as a ratio of the area of sun leaves) was 2.4 ± 0.10 ($r^2 = 0.85$), with no evidence of variation among forest or soil types (Table 7.1). A shift from big, shade-tolerant juvenile foliage to smaller adult foliage is observed in many tropical podocarps, especially canopy emergents, just as seen in temperate species.

SUCCESS IN MOUNTAIN ENVIRONMENTS

It is not surprising that podocarps are prominent in tropical montane forests: these are the environments most similar to temperate environments in which they evolved

as a group (Morley, this volume). Nitrogen and phosphorus are likely to be increasingly limiting in the mountains (Grubb, 1977), to the benefit of podocarps. Podocarps may be particularly effective at photosynthesis in the persistently cloudy conditions often encountered on tropical mountains. Using a physiological modeling approach, Whitehead et al. (2004) found that carbon uptake by *Dacrydium cupressinum* in lowland New Zealand is greater than that of oak trees in the United States when conditions are overcast and the diffuse fraction of incoming radiation is high.

There is little published information on regeneration processes and size structure of tropical montane podocarp populations (but see other chapters in this volume). *Podocarpus urbanii* in Jamaican montane rainforests is most common on less-fertile soils, although not on highly acidic mor soils (Tanner, 1977). It exhibits continuous regeneration in these forests but does not have a reverse-J distribution (Bellingham et al., 1995). Jamaican forests are frequently affected by hurricanes, but *P. urbanii*, like the two podocarp species in typhoon-affected Japanese forests, is resistant to hurricane disturbance (Bellingham et al., 1995). Following hurricanes, the growth rate of *P. urbanii* is faster than that of angiosperm trees, possibly because it survives storms relatively unscathed (Dalling et al., this volume; E. V. J. Tanner, University of Cambridge, personal communication). In addition, abundant seedlings and saplings of podocarps are found in the understory of high-altitude forests in New Guinea (Wade and McVean, 1969), suggesting that the species are sufficiently shade tolerant to regenerate under the canopy. Aiba et al. (2004) compared 42 common species, including four podocarps, in a plot at 1,560 m altitude in Kinabalu Park, Borneo. Two podocarp species were most common on ridges (*Phyllocladus hypophyllum* and *Dacrydium pectinatum*), whereas the other two were less restricted by topography

TABLE 7.1. Relationship of mean height and mean leaf area of canopy of leaves to forest and soil type. All data were extracted from descriptions provided by Earle (1997–2009); *N* is the number of species contributing to each mean. Leaf areas were estimated from mean widths and lengths assuming an elliptical shape, and the largest height was used whenever a range was given.

Forest type	Soil	<i>N</i>	Height (m)	Leaf area (cm ²)	Understory to canopy tree leaf area ratio
Tropical lowland	Poor soils	9	14.9 ± 2.8	4.7 ± 1.7	3.2 ± 0.8
	Mostly poor	11	25.5 ± 5.1	5.1 ± 3.5	3.1 ± 0.8
	Better soils	8	27.5 ± 4.8	9.0 ± 3.4	3.3 ± 1.3
Tropical montane and warm temperate	Poor soils	17	19.2 ± 2.7	1.9 ± 0.8	4.1 ± 0.6
	Mostly poor	14	24.6 ± 3.8	4.7 ± 1.6	2.3 ± 0.3
	Better soils	9	26.2 ± 3.6	4.1 ± 1.5	3.1 ± 1.0
Cool temperate	All soils	25	14.9 ± 2.8	1.1 ± 0.5	4.3 ± 0.9

(*Dacrycarpus imbricatus* and *Falcatifolium falciforme*). All podocarp species except *Falcatifolium falciforme* had a greater proportion of their crowns in exposed positions within the canopy than predicted by chance, suggesting that they were light demanding. In contrast, *Falcatifolium falciforme* had a greater proportion of its crowns in shaded positions and a population structure indicating that the species was shade tolerant (Kitayama et al., this volume).

RARITY IN LOWLAND TROPICAL SITES ON BETTER SOILS

Podocarps are absent from much of the lowland tropics, except on poor soils, although they are rare components of Australasian tropical lowland and lower montane forests (Enright, 1995). Two widespread species, *Podocarpus neriifolius* and *Nageia wallichiana*, reach densities of only 1–2 per hectare within the 700–1,500 m elevation band of New Guinean mountains and are usually observed as solitary trees with few seedlings nearby (Enright, 1995). We reason that three factors conspire to exclude podocarps: (1) The high leaf area index of the lowland tropical forests means that the understory is too deeply shaded to allow even the most shade tolerant of podocarps to regenerate, the exception being *Nageia* species, which have large, multiveined leaves (mean for lowland species = 48 cm²) similar to those of *Gnetum* (another gymnosperm of rainforest understories). (2) Podocarps are outcompeted in the race for light in tree fall gaps. Tropical podocarps may well grow faster than temperate relatives—their wood contains wider tracheids (Lusk, this volume) and is significantly less dense (Figure 7.1)—but it is inconceivable that they could compete with the growth of light-demanding angiosperms, which can reach upward of 1 m a year (e.g., Richards and Williamson, 1975). For example, a gap-demanding angiosperm, *Toona australis*, was found to have greater stomatal conductance and leaf-specific stem hydraulic conductivity than two tropical podocarps (*Nageia fleuryi* and *Podocarpus grayii*) and grew much more rapidly than the podocarps in full sun (1,300–1,800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Brodribb et al., 2005). Finally, (3) opportunities for catastrophic regeneration are taken by angiosperms. Among the lowland tropical podocarps, two New Caledonian trees, *Dacrycarpus vieillardii* and *Podocarpus polyspermus*, appear to be exceptions and are maintained by disturbance, colonizing floodplains in a way similar to *D. dacrydioides* and *P. totara* in New Zealand (Jaffré, 1995). For most of the lowland tropics this niche is taken by angiosperm trees, some of which are long-lived (e.g., *Ceiba pentandra*). Other regeneration niches associated with disturbance seem to be taken by angiosperms. For example, the “shade-persistent

pioneer” strategy of the long-lived angiosperm tree *Alseis blackiana* in lowland rainforests in Panama (Dalling et al., 2001) is analogous to some long-lived podocarps (e.g., *Podocarpus totara*) in New Zealand rainforests.

Most tropical podocarp species are intolerant of fire, like their temperate cousins. In the Dominican Republic, fire virtually excludes *Podocarpus aristulatus* from forests above 1,800 m, which are dominated by *Pinus occidentalis*. Fires are prevalent during El Niño droughts in these forests (every seven years or so), and they also have lower temperatures and precipitation than the cloud forests at lower altitude (1,550–1,800 m), which do not support fire and in which *P. aristulatus* is the third commonest tree (Martin and Fahey, 2006; Martin et al., 2007). Similarly, the páramo grasslands of the Andes have spread in response to frequent burning during the last 8,000 years, and podocarps are now restricted to montane forests well away from the grasslands (Niemann and Behling, 2008). Increased fire frequency since the arrival of humans is thought to be the major driver of podocarp extinction in Australia (e.g., *Dacrydium* from tropical north Queensland; Lynch et al., 2007). A few tropical podocarp species are capable of persisting in habitats that burn. *Dacrycarpus compactus*, *Dacrycarpus expansus*, and *Dacrydium novo-guineense* are all locally prominent components of tree fern grasslands and thickets that occur near tree lines on tropical mountains, even though indigenous peoples burn these areas. Corlett (1984) noted that *Dacrycarpus compactus* has thick bark, which might afford it some protection.

CONCLUDING THOUGHTS

Tropical and temperate podocarps function much as Bond envisaged: they are slow-growing tortoises. Most tropical species are restricted to montane forests with low total leaf area or lowland sites with exceptionally poor soils. Competition for light is less intense in such forests, and podocarps compete effectively by efficient capture and retention of nutrients. In addition, genera with small leaves held on erect/pendent stems may also achieve high rates of whole-plant photosynthesis in open canopied forests that prevail on poor soils. On richer soils in the tropics, slow-growing podocarps are incapable of competing with angiosperms in the battle for light in tree fall gaps. Some species may be capable of tolerating deep shade and surviving for many years in forest understories, but regeneration is not possible unless there is significant height growth, and that is severely hampered by shading. The simplest hypothesis is that the leaf area indices of lowland tropical forests are simply too high to allow regeneration

of imbricate-leaved podocarps, whereas broad-leaved species with anastomosing veins (*Nageia* and some *Podocarpus*) are so shade tolerant that they regenerate beneath closed canopies. Measurement of growth and survival of podocarps in contrasting tropical forest types, in conjunction with demographic models (e.g., Kunstler et al., 2009), would help resolve this issue.

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APPENDIX: DESCRIPTIVE ACCOUNTS OF PODOCARPS FROM TROPICAL, SUBTROPICAL, AND WARM TEMPERATE REGIONS

Descriptions are taken primarily from Earle (1997–2009), who sourced his data from various primary references, and also from personal communications with P. J. Grubb. Information on Andean and Amazonian species in the last section was sourced from Jorgensen and Leon-Yanez (1999). Tree heights (*H*) are given after each description; where a range of heights for different habitats is published, the largest is quoted.

LOWLAND TROPICAL RAINFORESTS

Common on Poor Soils but Not Restricted to Them

Dacrycarpus vieillardii. New Caledonia. Grows throughout the main island on serpentine soils along riverbanks, in moist depressions, and in frequently flooded areas from sea level to 900 m above sea level. Similar in ecology to *D. dacrydioides* of New Zealand. *H* = 25 m.

Dacrydium balansae. New Caledonia. Occurs in the drier parts of forests, normally on serpentine soils from sea level to 1,000 m. A few specimens from ombrophilous forest were 20 m tall trees. *H* = 12 m.

Dacrydium guillauminii. New Caledonia. Found within a few kilometers along two rivers. *H* = 2 m.

Dacrydium magnum. Solomon Islands, Moluccas. Locally common in the canopy of moist tropical forest between 60 and 1,200 m. Often along ridge crests, where it has a somewhat reduced stature. *H* = 30 m.

Dacrydium nidulum. Fiji, New Guinea, Moluccas, Celebes, Lesser Sunda Islands. Common in the western parts of New Guinea, but elsewhere populations are mostly rather isolated. A canopy tree of primary and sometimes secondary rainforest from sea level to 1,200 m, but mostly under 600 m. In Fiji it forms open, low-growing, monodominant stands of stunted trees and is also a component of mesic forests (Keppel et al., 2006). *H* = 30 m.

Dacrydium pectinatum. Hainan, China, Malesia, Borneo, Philippines. Scattered large individuals are found in primary rainforest other than dipterocarp forest from sea level to 1,500 m, but mostly below 600 m. Dense stands are found in boggy areas, and nearly pure stands of stunted trees occur in shallow sandy soils, especially on degraded heath forests (“padangs”) and on kerangas in heath forest. In Sabah it grows on ultramafic soils; in Brunei it grows in pure stands in the center of peat swamps. *H* = 40 m.

Nageia maxima. Borneo (Sarawak). Locally common in the understory of rainforest on ridges in Bako National Park and in the peat swamp forest, from ~0 to 120 m. *H* = 10 m.

Nageia motleyi. Southern Thailand, Malesia (Malaya, Sumatra, Borneo). Scattered in primary and secondary rainforest, from very low altitude (15 m) to ~500 m. Occurs not only on slopes and hills on dry soil but also in Borneo in other situations: in Sarawak on deep peat in a mixed ramin-peat swamp, on ridges and hillsides in bindang-dipterocarp forest, and at 1,000 m on podsolic sandy loam. *H* = 54 m.

Podocarpus confertus. Malesia. Subdominant in somewhat open and sometimes stunted forest. Found in dense local populations on various poor soils, some or most of which are ultrabasic. *H* = 36 m.

Podocarpus insularis. New Hebrides, Solomon Islands, New Britain, New Guinea and adjacent islands. Scattered and locally common in wet rainforest, also in *Nothofagus* forest with undergrowth of *Nastus* from near sea level to 1,680 m, and as smaller trees in low ridge habitats. *H* = 39 m.

Podocarpus neriifolius. Nepal, Sikkim, India, Thailand, Vietnam, Malaysia, Indonesia, Philippines, Celebes, Lesser Sunda Islands, Moluccas, New Guinea, New Britain, Solomon and Fiji islands. Scattered and locally common in primary rainforests from near sea level to ~2,100

m. In most areas it appears as an understory tree with occasionally much larger, emergent specimens in the canopy, but in other areas it is normally a canopy tree. Various habitats (often on rocky hilltops, in mossy forest, and swampy forests but rarely riverine) and on various soils (limestone, kerangas in heath forest, sandstone ridges, and laterites, sandy clay, ultrabasic). *H* = 30 m.

Retrophyllum minus. New Caledonia. Southern part of island on ultramafic soils, at elevations of up to 200 m above sea level. A water-dependent plant (rheophyte) inhabiting riparian habitats, in this case lakes and riverbanks in shallow water. *H* = 3 m.

Restricted to Poor Soils or Open Forest

Dacrydium araucarioides. New Caledonia. Locally, a dominant species in the vegetation on serpentine soils, from sea level to 1,150 m. *H* = 6 m.

Dacrydium elatum. Vietnam, Laos, Cambodia, Thailand, Malaya, Sumatra, Borneo. Scattered in moist rainforest, from sea level but mostly above several hundred meters to 1,700 m. Grows most abundantly in open situations, indicating a preference for disturbed conditions. It also appears to prosper on difficult soils (sandstone, granite, kerangas). Does not enter into high mountain scrub. *H* = 40 m.

Dacrydium nausoriense. Fiji. In slightly open forest on the leeward sides of the large islands of Fiji and apparently of limited extent. *H* = ?

Falcatifolium angustum. Borneo. Found at 90–240 m on podsolized sands and kerangas. *H* = 20 m.

Falcatifolium falciforme. Malaya, Borneo. Locally common along ridges as a bushy tree or in the subcanopy of primary rainforest, often on podsolized sands and kerangas, but occasionally on deeper fertile soils. Somewhat emergent forest giant, from 400–2,100 m. *H* = 12 m?

Podocarpus beecherae. Southern New Caledonia. Maquis vegetation on ultrabasic soil (generally toxic to plants and the reason for the stunted plants of the maquis) at low elevation. *H* = 6 m.

Podocarpus costalis. Philippines and other islands between Luzon and Taiwan. On coastal bluffs from sea level to at least 300 m elevation. *H* = 5 m.

Podocarpus globulus. Borneo. Found in primary rainforest or moss forest on ridges and peak at 300–1,500 m elevation in areas where the forest is not dominated by dipterocarps. Adapted to ultramafic soils. *H* = 27 m.

Podocarpus micropedunculatus. Borneo. From 0 to 500 m elevation scattered in *Agathis* forest understory or in thickets at the edges of clearings. Mostly on sandy,

podzolic soils, kerangas, sandstone, humic peaty podzols of raised beaches, and peat swamp forests. *H* = 7 m.

Podocarpus polystachyus. Thailand, Malaysia (Malay Peninsula), Borneo, Philippines, Moluccas, west New Guinea. Mainly at low altitudes in three distinct habitats: (1) sandy beaches, often gregariously bordering the sea at high-tide mark, sandy coastal bluffs and low outcrops, and also sandy ridges in mangroves; (2) on lowland coastal kerangas and sandy pandangs (degraded heath forest) and sandy heath forest; and (3) on limestone hills inland. *H* = 20 m.

Podocarpus teysmannii. Malaysia, Indonesia. An understory tree in primary or secondary rainforest at elevations up to 1,140 m. In Banka it grows on granite sands. *H* = 12 m.

Apparently Associated with Rainforests on Relatively Fertile/Deep Soils (No Mention of Poor Soil in Description)

Nageia fleuryi. China (Guangdong, Guangxi, and Yunnan), Cambodia, Laos, Vietnam (mountainous provinces). Occurs sparsely in primary and slightly disturbed evergreen rainforests at elevations of 200–1,000 m. At Cuc Phuong and Cat Ba National Parks, the species occurs in groups and is the main species in some stands. A light-demanding species thriving well on good sites with deep, well-drained soils developed from limestone. *H* = 25 m.

Nageia nagi. Japan, China, Vietnam. Grows in tropical evergreen broad-leaved forest, on hills or mountains below 1,000 m elevation. Neutral, shade-demanding tree when young. When mature, may become a canopy dominant. Associated with ferrallitic, deep and fertile, loamy-sandy soils. *H* = 30 m.

Nageia wallichiana. India (Assam), Burma, Thailand, Indochina, China (Yunnan), Malesia (Sumatra, Malaya, Banka Island, western Java, Lesser Sunda Islands, Borneo, Philippines, north and central Celebes, Moluccas), New Guinea. Scattered and often common (but nowhere reported as gregarious or dominant) in primary rainforests from very low elevation (5 m), ascending occasionally as high as 2,100 m. Widely distributed in southern China, growing on neutral or slightly acidic soils, tolerating shade. One of the tallest trees in the forest, but perhaps barely emergent. *H* = 54 m.

Parasitaxus usta. New Caledonia. Found at 400–1,100 m elevation. This is the only known parasitic gymnosperm. *H* = 1.8 m.

Podocarpus ledermannii. New Guinea, New Britain. Scattered and locally common in the understory of

primary rainforest from low elevation to at least 1,800 m. $H = 26$ m.

Podocarpus levis. Eastern Borneo, Celebes, Moluccas, New Guinea. Scattered and locally common in primary rainforest, from sea level to 1,650 m. In eastern Borneo on limestone. $H = 25$ m.

Podocarpus nakaii. Taiwan. Scattered as a subcanopy tree in broad-leaved forests in the northern and central parts of the island. $H = ?$

Podocarpus spathoides. Solomon Islands, eastern New Guinea, northern Moluccas, Malaya. Scattered and locally common at 1,000–1,200 m in the two western stands and near sea level in the east. Recent field work indicates that "*P. spathoides*" in the Solomon Islands (which occurs at sea level) is sufficiently distinct to be described as a new species (M. Gardner, Royal Botanic Garden Edinburgh, personal communication). $H = 30$ m.

Podocarpus spinulosus. Australia (New South Wales and Queensland). A shrub in sheltered coastal sites and gullies on the adjacent ranges. $H = 3$ m.

MONTANE TROPICAL RAINFORESTS

Common on Poor Soils but Not Restricted to Them

Dacrycarpus cinctus. Central Celebes, Moluccas, New Guinea. In New Guinea extremely common and often dominant or codominant with *Nothofagus*, *Libocedrus*, *Elaeocarpus*, and *Podocarpus*, in mountain forest and mossy forest. On Mount Binaja in orchard-like pure stands with a mossy ground cover. Rarely in muddy parts of swamps. A canopy tree or sometimes emergent, often thick trunked at 1,800–2,850 m. Occasionally reaches 3,600 m; in Ceram occurs at 1,300–3,000 m. $H = 33$ m.

Dacrycarpus compactus. New Guinea. In subalpine shrubberies and alpine grasslands, 3,200–3,800 m. Common on the higher peaks near the tree line, sometimes forming pure stands, emerging above a subalpine shrubbery, or scattered in alpine grassland often as isolated specimens and obviously fire resistant. A component of *Podocarpus*–*Libocedrus* forest, rarely on wet peaty soil, at 2,800–3,950 m, but mostly above 3,400 m. $H = 20$ m.

Dacrydium beccarii. Solomon Islands, New Guinea, Moluccas, Philippines, Borneo, Malaya, northern Sumatra. In the eastern part of the range there are only widely separated occurrences, and even in the western part they are somewhat discontinuous. Most common as a shrub or small tree on mossy ridges where it is often dominant, but also found rising above a low, mixed mountain scrub at 600–2,500 m. A variety of soils have been indicated. $H = ?$

Dacrydium gibbsiae. Borneo. Common on the slopes, being codominant on ultrabasic soils in the mountain mossy forest at 1,500–3,600 m. $H = 12$ m.

Dacrydium gracile. Borneo, Sarawak. Rows scattered in the canopy of mountain rainforest. In Sarawak also in heath forest on sandstone. Rare. $H = 30$ m.

Dacrydium xanthandrum. Solomon Islands, New Guinea, Celebes, Philippines, Borneo, northern Sumatra. Locally discontinuous. Locally common or even dominant and shrubby on mossy ridges with peaty soils over clay, sand, granite, sandstone, or dacite. Also scattered as trees in nearby primary forest from (500–)1,000–2,700 m. $H = ?$

Falcatifolium taxoides. New Caledonia. An understory tree in the wet forests on ultramafic soils of the main island. $H = 15$ m.

Phyllocladus hypophyllus. Philippines, Borneo, Celebes, Moluccas, New Guinea. Moist mountain forests sometimes as low as 900 m up to the tree line at 3,200–4,000 m. Scattered in the forest at lower elevation where trees may be quite large. More common but of reduced stature at higher elevations. In New Guinea it is a widespread and common species from the upper lowland forests to the subalpine shrubberies, rarely as a solitary tree in the alpine grasslands (900–3,600 m). $H = 30$ m.

Podocarpus laubenfelsii. Borneo, Sabah, eastern Kalimantan. Scattered in primary rainforest and moss forest, growing as a large emergent on rocky ridges on kerangas. Dominant in heath forests and on waterlogged acid soils of *Agathis* forests. $H = 35$ m.

Podocarpus pseudobracteatus. New Guinea. Scattered and locally common in the understory of mossy *Castanopsis*–*Nothofagus* forest and *Dacrydium* swamp forest, sometimes entering the alpine shrubbery. $H = 15$ m.

Podocarpus rotundus. Eastern Borneo, Philippines. Found in dwarf mossy forest, at about 1,000–2,200 m. $H = 15$ m.

Podocarpus rubens. Sumatra, Celebes, Lesser Sunda Islands, New Guinea. Scattered as a medium-sized tree in primary rainforest, mostly above 1,500 m but as low as 800 m on smaller islands. Otherwise locally common to dominant as a small tree on ridges at 2,000–3,000 m or occasionally higher. Mostly on latosols. In New Guinea in fagaceous mossy forest, rarely in swampy forest on peaty soils with *Dacrydium*. $H = 30$ m.

Podocarpus smithii. Australia (Queensland). Endemic and highly local in montane rainforests on the eastern Atherton Tableland. Usually grows along creeks at mid elevations (900–1,200 m), often on granitic soils. $H = 30$.

Podocarpus urbanii. Jamaica. Montane rainforests of the Blue Mountains (1,370–2,250 m) across most soil

types, but most abundant on those of low, but not lowest, available nitrogen and phosphorus. $H = 15$ m.

Sundacarpus amarus. Australia (northeastern coastal Queensland), New Guinea, Moluccas, Lesser Sunda Islands, Java, central and southwestern Celebes, Philippines, Borneo, Sumatra. In Queensland primarily in the Atherton Tableland on basaltic soils at 600–1,200 m. Scattered and often common in primary and secondary rainforest. Very common in New Guinea, often in fagaceous forest, sometimes in mossy forest or submontane forest at ~900 m (with *Dysoxylum*, *Macaranga*, and *Ficus*), where it can be emergent as a colossal tree. Often on latosols, rarely on sandy soils or on marshy ground. Occurs from sea level but mainly at 500–2,000 (–2,300) m. $H = 60$ m.

Restricted to Poor Soils or Open Forest

Dacrydium comosum. Malaya. On exposed ridges as a local dominant in stunted mossy forest at 1,440–2,200 m. $H = 4$ m.

Dacrydium ericoides. Malesia. Locally common in primary forest on exposed mossy ridges at 1,000–1,500 m. $H = 17$ m.

Dacrydium lycopodioides. New Caledonia. At elevations of 900–1,400 m in ombrophilous forests on the southern part of the main island. $H = 25$ m.

Dacrydium medium. Malaya, northern Sumatra. Shrub or small tree rising above and often dominant in low mountain scrub on what appears to be rather poor soils at 960–2,100 m in Malaya and 1,800–2,600 m in Sumatra. $H = ?$

Dacrydium novo-guineense. Celebes, Moluccas, New Guinea. Long, mossy crests and in open areas at 700–3,000 m, but mostly 1,500–2,200 m. Rising above the mid-mountain canopy or a common small tree at higher elevations rising above ferns and other scrub often after fire. Sometimes dominant. On different soil types: clay, stony sand. $H = 29$ m.

Falcatifolium gruezoii. Philippines, Celebes, Moluccas. In exposed locations along ridges or on the borders of open areas. At 1,600–2,200 m in the Philippines, 1,200–1,400 m in Celebes, and 700 m in Obi (Moluccas). $H = 12$ m.

Podocarpus archboldii. New Guinea. Mainly found in upper lowland regions to upper montane areas and occasionally in the subalpine shrubberies (800–3,100 m). $H = 40$ m.

Podocarpus brassii. New Guinea. Usually found in upper montane and subalpine regions, sometimes venturing out into the alpine grasslands. Also as a survivor of burned subalpine shrubberies replaced by grassland. $H = 15$ m.

Podocarpus crassigemmis. New Guinea. Common or subdominant in the canopy of high-mountain mossy forest

or emergent. Often in *Nothofagus* and *Phyllocladus* forest, rarely in secondary forest, and occasionally in grassland. $H = 38$ m.

Podocarpus deflexus. Malaysia (northern Sumatra, Malaya). Rising above and locally dominant in dwarf mountain scrub at 1,500–2,100 m. $H = 10$ m.

Podocarpus gibbsiae. Borneo. At 1,200–2,400 m elevation, typically on moss forest ridges. Mostly or always on ultramafic soils. $H = 20$ m.

Podocarpus glaucus. Solomon Islands, New Guinea, Moluccas, Philippines. A medium-sized tree in the forest or more often dwarfed or even decumbent on mountain crests in stunted mossy forests. Often locally common, (500–)1,000–2,800 m. Recorded from stony, sandy clay and from a limestone ridge associated with *Gymnostoma* and *Rhododendron* on peaty soil. $H = 15$ m.

Podocarpus gnidioides. New Caledonia. Above 600 m elevation on rocky ridges in the mountains. $H = 2$ m.

Podocarpus ridleyi. Malaysia. Localized and more or less dominant on several isolated peaks with poor soils in a somewhat stunted rainforest, at 480–1,300 m. On ridges over sandstone and on granite. $H = 24$ m.

Retrophyllum comptonii. New Caledonia. Ombrophilous forests on ultramafic soils throughout the main island at 750–1,450 m. $H = 30$ m.

Apparently Associated with Rainforests on Relatively Fertile/Deep Soils (No Mention of Poor Soil in Description)

Dacrycarpus imbricatus. Northern Burma, far southern China, Vietnam, Laos, Malaya, Philippines, Sumatra, Borneo, Java, Celebes, Moluccas, Lesser Sunda Islands, New Guinea, New Hebrides, Fiji. Mostly scattered and common in primary and secondary rainforest. In West Java codominant with *Podocarpus neriifolius* and *Altingia noronhae*, on the south slope of Mount Tjeremai volcano characterizing the zone between 2,400–2,700 m, unexplainably without other codominants. In Timor found under more or less seasonal conditions as isolated specimens laden with *Usnea* in grassland after deforestation, mostly at 1,000–2,500 m. In Lombok reported at as low as 200 m, and in Celebes ascending to 3,000 m. Probably exterminated at lower elevations by deforestation. In China in mixed forests or pure stands on slightly acidic yellow earth soils in valleys of montane streams at 400–1,500 m. $H = 50$ m.

Dacrydium spathoides. New Guinea. Growing as a canopy tree at 2,150–2,200 m in moist, mossy mountain rainforest. $H = 34$ m.

Falcatifolium papuanum. New Guinea. Grows in the understory of moist mountain forests at 1,500–2,400 m. Typical associates include *Nothofagus*, Myrtaceae, and other Podocarpaceae. $H = 22$ m.

Podocarpus dispersus. Australia (Atherton Tableland). In rainforest, not plentiful. $H = 20$ m.

Podocarpus macrocarpus. Philippines. Scattered and sometimes common in cloud forests, ~2,000–2,100 m. $H = 20$ m.

Podocarpus macrophyllus. Southern Japan, Burma, China, Taiwan. Virgin broad-leaved forest dominated by over 20 m tall trees of Lauraceae and Fagaceae. $H = 15$ m.

Podocarpus magnifolius. Eastern Venezuela to Bolivia. Widely distributed in cloud forest at 800–1,600 m. $H = 25$ m.

Podocarpus neriifolius. Vietnam. Occurs as scattered individuals in remaining primary forests in remote areas, growing sparsely along water courses, usually mixed with broad-leaved species, such as *Fokienia hodginsii*, *Celtis australis*, *Altingia siamensis*, *Cinnamomum* spp., *Gironiera subaequalis*, *Mallotus yunnanensis*, *Castanopsis*, and *Lithocarpus* spp. It chiefly appears on humid, fertile, especially sandy soils, but also on clayey-stony soils. $H = 25$ m.

Podocarpus rumphii. Philippines, Taiwan. Scattered in broad-leaved forests at medium altitudes. $H = 30$ m.

Prumnopitys ladei. Australia (Atherton Tableland, Queensland). Rainforests on granite-derived soils at 1,000–1,200 m. $H = 25$ m.

Retrophyllum rospigliosii. Western Venezuela, Eastern Colombia, central Peru. Native to the wet forests of the Andes, it grows best at 500–3,500 m, needing constant humidity and cloudiness. Develops best on gentle slopes, fertile river lowlands, plateaus, and small depressions. Grows in wet, clay or clay-sand, deep, relatively fertile soils with good to slow drainage and acidic pH. $H = 30$ m.

INSUFFICIENT INFORMATION AVAILABLE

Dacrycarpus cumingii. Widespread in Philippines, northern Sumatra; rare in Borneo. Locally common at elevations of (1,000–)1,850–2,650(3,314) m in primary moss forest. $H = 25$ m.

Dacrycarpus expansus. Papua New Guinea (Central Highlands). Locally common or even in pure stands or codominant, sometimes emergent. Often in (human) disturbed situations, such as on edges of tree fern grassland, 1,300–2,750 m. $H = 25$ m.

Dacrycarpus kinabaluensis. Borneo. Common, growing in sometimes pure stands in dwarf mountain scrub at

elevations from about 2,700 m to the tree line at about 4,000 m. $H = 13$ m.

Dacrycarpus steupii. Central eastern Borneo, central Celebes, New Guinea. Locally common, particularly in disturbed forests, or in poorly drained areas where it may form nearly pure stands. In boggy grasslands and reed swamps, on sandy clay, once on a rocky riverbank, once on a limestone hillock in mossy forest (Mount Beratus). Elevations of 860–3,420 m, but mostly ~1,500–2,000 m. $H = 35$ m.

Dacrydium cornwallianum. New Guinea. Dominant to nearly pure stands in swamp forests and perhaps also mossy heath forests at 1,450–2,300 m. $H = 30$ m.

Dacrydium leptophyllum. Western New Guinea. Known only from the top of Mount Goliath at 3,000–3,600 m. $H = ?$

Prumnopitys standleyi. Costa Rica. At 2,000–3,200 m, in areas with 2,000–4,000 mm annual rainfall and temperature range of 3°C–25°C. $H = 25$ m.

Podocarpus sellowii. Brazil. Extremely broad and scattered range, occurring in montane vegetation. Typical of montane areas in the tropical coastal range rainforest (Mata Atlántica) and rarely occurs within *Araucaria angustifolia* forests. $H = ?$

Podocarpus acuminatus. Brazil. $H = 4.5$.

Podocarpus atjehensis. Northwestern Sumatra, New Guinea. $H = 15$ m.

Podocarpus borneensis. Borneo. Locally common or even dominant on mossy rocky ridges or scattered in nearby forest, in high kerangas forest and on white, sandy soils. Elevations of 700–2,070 m; one collection from a swamp at 360 m. $H = 12$ m.

Podocarpus bracteatus. Indonesia, Java, Lesser Sunda Islands. $H = 40$ m.

Podocarpus brasiliensis. Brazil, Venezuela. Mountains and in few hectares of wetland in the middle of the massive Cerrado. $H = 15$ m.

Podocarpus brevifolius. Philippines, Indonesia, China (Guangxi and Guangdong), Vietnam. Usually growing on limestone. $H = 15$ m.

Podocarpus buchholzii. Venezuela. $H = 7$ m.

Podocarpus glomeratus. Andes. Elevations of 2,500–4,000 m. $H = ?$

Podocarpus ingensis. Andes. Elevations of 1,000–3,000 m. $H = ?$

Podocarpus lambertii. Argentina, Brazil. $H = ?$

Podocarpus lophatus. Philippines. Mossy forest at 1,800 m elevation. $H = ?$

Podocarpus matudae. Mexico, Guatemala. Large tree. $H = ?$

Podocarpus roraimae. Mountains bordering Venezuela and Guyana. Endemic. Elevations of 1,800–2,400 m. *H* = ?

Podocarpus sprucei. Andes. Elevations of 2,000–4,000 m. *H* = ?

Podocarpus steyermarkii. Venezuela, Guyana. *H* = 25 m.

Podocarpus tepuiensis. Eastern Venezuela. Endemic shrub or small tree. *H* = ?

Podocarpus woltzii. Madagascar. *H* = 20 m.

Prumnopitys montana. Andes. Elevations of 1,500–4,000 m. *H* = ?

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Ecology of Fire-Tolerant Podocarps in Temperate Australian Forests

Philip G. Ladd and Neal J. Enright

ABSTRACT. *Podocarpus drouynianus* and *P. spinulosus* are two unusual conifers restricted to southwestern and eastern Australia, respectively. The species are morphologically similar and genetically closely related to each other but rather distant from other members of the subgenus *Foliolatus*. Both species have retained ancestral podocarp characteristics such as dioecy, wind pollination, and large, animal-dispersed seeds with recalcitrant germination. They also thrive on soils with generally low nutrient content. However, they have several innovations that ensure their success in an environment that would generally be considered unsuitable for podocarps. Both species have much higher leaf length to width ratios than other *Podocarpus* species: this presumably aids their survival on low- to moderate-rainfall sites. They both resprout strongly after fires, and at least for *P. drouynianus*, seed production is cued by defoliation, and sporophylls are produced most prolifically on new growth one year after fire. The species are unique in the genus as being successfully adapted to a relatively dry, fire-prone environment.

INTRODUCTION

In almost all parts of the world where the genus occurs, the archetypical *Podocarpus* is a single-stemmed rainforest or riparian tree that is fire sensitive. However, in temperate mainland Australia two fire-tolerant shrub podocarps represent radical departures from this model. In *Ecology of the Southern Conifers* (Enright and Hill, 1995), a chapter on conifers of southern Australia (Gibson et al., 1995) noted that little was known about the ecology of several of the temperate Australian conifers, particularly *P. drouynianus* from southwestern Australia, and the eastern equivalent species (*P. spinulosus*) is not even mentioned. Only *P. drouynianus* has any commercial importance and is used as a “background foliage filler” in the cut flower industry in Western Australia. Since 1995, little has changed concerning our knowledge of the ecology of these two species, although one paper has been published on seed production and recruitment of *P. drouynianus* (Chalwell and Ladd, 2005).

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The two species are classified in *Podocarpus* subgenus *Foliolatus* and in cladistic analyses are found in a clade sister to the remaining members of the subgenus (Biffin et al., this volume). Almost all other species in the subgenus are tall forest trees, although there are a few species of lower stature that grow at high altitudes in Asia. Both species grow in lowland eucalypt forest rather than rainforest and retain many of the normal attributes of *Podocarpus*, including seed, leaf, and root morphology. However, in other respects they are similar to the much more widespread sclerophyllous Australian flora with which they co-occur. This chapter describes the ecology of these fire-tolerant species and highlights the adaptations that have enabled them to survive in environments that at first impression would not be expected to support podocarps.

METHODS

Herbarium records and personal observations of plant locations for *P. drouynianus* and *P. spinulosus* were used to produce distribution maps and BIOCLIM analyses. BIOCLIM is a computer modeling system that uses bioclimatic parameters derived from mean monthly climatic estimates to predict climatic conditions at any specified location (Busby, 1986). Using a digital elevation model and parameters such as latitude, longitude, and altitude, the climatic envelope of a species can be predicted. BIOCLIM was used to examine the climatic envelope of these two podocarp species. Mean bioclimatic details for the two species were statistically compared with a *t* test (or Mann Whitney U test if the data failed to satisfy requirements for parametric testing). Population size and structure were measured in the field in plots of various sizes, depending on the density of plants and in order to obtain a sufficient number of plants to gain a representative sample. Since these species are lignotuberous multi-stemmed shrubs, size class structures were based on number of stems for plants up to 10 stems and then the circumference of the lignotuber for larger plants. This was considered the most appropriate procedure because stem number varies with time since fire and also because longest diameter often did not reliably represent the size of the lignotuber if its outline was irregular.

SEED MASS, SEED PRODUCTION, AND GERMINATION RATE

Seed mass was determined for seeds collected from populations of *P. drouynianus* at Jalbarragup and Nannup, south of Perth, and from a population of *P. spinulosus* at

Pearl Beach, near Sydney. Seed production was examined for populations of *P. drouynianus* at Jalbarragup and Sawyers Valley, east of Perth.

Seed from natural populations at Jalbarragup and collected from garden-cultivated plants of *P. spinulosus* was germinated on the surface of soil in seed trays in controlled-temperature cabinets at 5°C temperature intervals between 15°C and 35°C and, for seeds subject to cold stratification, at 4°C (20 seeds × 5 replicates). Large seed size prevented good contact with the moist surface of filter paper, and being partially impressed into the soil surface provided a better moisture contact with the seed, so that germination on soil was the preferred method for germination testing. Whereas seed germination for many species in the fire-prone sclerophyll forests of southern Australia is enhanced by the effects of heat and/or smoke associated with fire relative to rates in the absence of these cues (Enright et al., 1997), the postfire pattern of seed production in *P. drouynianus* suggested that no fire-related stimulus is required for germination, and initial germination testing assumed no such requirement.

STEM AND LEAF MEASUREMENTS

The timing and extent of lignotuber development was examined in seedlings from seed collected at Pearl Beach and Jalbarragup. Stem outgrowths in *P. spinulosus* were studied by microscopic examination of stem sections fixed in a mixture of formalin, acetic acid, and alcohol, then embedded in plastic for sectioning and stained with toluidine blue.

Leaf dimensions of *P. drouynianus* and *P. spinulosus* were compared with published measurements from other species in the subgenus *Foliolatus*. Our hypothesis was that as the two Australian species grow at the arid end of the podocarp climatic spectrum, they should have narrower leaves than most of the other species, which generally occur in much wetter environments. Leaf measurements were derived from the mean value on the basis of dimensions given for species listed on the Gymnosperm Database Web site (<http://www.conifers.org/po/po/index.htm>; accessed 7 July 2009) for *P. spinulosus* plants grown in Perth and *P. drouynianus* from plants collected in the field near Nannup.

POPULATION STRUCTURE

Size structure in *P. drouynianus* is reported for two populations (Jalbarragup and Sawyers Valley; see Chalwell and Ladd, 2005, for full details of populations and sampling methods) and in *P. spinulosus* for four populations, two at Pearl Beach (Crommelin 1 and 4), plus single

TABLE 8.1. Location, details, and attributes for the sites mentioned in the text. Abbreviations: NSW, New South Wales; WA, Western Australia.

Site name	Location	Elevation (m)	Geology	Soil	Vegetation
Pearl Beach	NSW, 33°32'S, 151°18'E	20	Sedimentary sands	Sand	Eucalypt open forest
Sydney Botanic Gardens	NSW, 33°33'S, 151°13'E	20	Sandstone	Skeletal sandy soil	Cultivated garden
Yalwal	NSW, 34°11'S, 150°37'E	200	Sandstone	Skeletal sandy soil	Eucalypt open forest
Burrill Lake	NSW, 35°22'S, 150°26'E	20	Sedimentary sands	Sand	Eucalypt open forest
Sawyers Valley	WA, 31°55'S, 116°13'E	250	Lateritized granite	Red brown earth	Eucalypt open forest
Nannup	WA, 33°59'S, 115°45'E	210	Lateritized granite	Red brown earth	Eucalypt open forest
Jalbarragup	WA, 34°03'S, 115°37'E	150	Lateritized granite	Red brown earth	Eucalypt open forest

populations at Lake Burrill and Yalwal (Table 8.1). Plants were divided into classes by size: the first two categories were by number of stems (1–2 and 3–10), and plants with more than 10 stems were then divided into 20 cm (*P. spinulosus*) or 50 cm classes (*P. drouynianus*).

RESULTS

SPECIES DISTRIBUTION

Podocarpus spinulosus and *P. drouynianus* are endemic to eastern and southwestern Australia, respectively, in areas relatively close to the coast, where rainfall is generally higher and risk of frosts lower than for sites farther inland at the same latitude. *Podocarpus spinulosus* extends over a much greater latitudinal range (approximately 24°S–36°S) than *P. drouynianus* (32°S–35°S; Figure 8.1), and although the overall climate profiles of the two species are similar (e.g., no significant difference in mean annual rainfall between habitats: *P. drouynianus*, 1039 ± 26 mm; *P. spinulosus*, 1115 ± 59 mm), there are several significant differences between them in other bioclimatic details (Table 8.2). Mean annual temperature is significantly lower for *P. drouynianus* than for *P. spinulosus*, and precipitation in the warmest quarter is significantly lower for *P. drouynianus* but is the reverse for the coolest quarter, reflecting the strong Mediterranean-type climate experienced by *P. drouynianus*.

SEED PRODUCTION AND GERMINATION

Plants of both species are dioecious. The seeds are borne on a “podocarpium,” colored deep purple when

ripe. Seed mean fresh mass for *P. spinulosus* is significantly lower (0.24 ± 0.01 g, Pearl Beach population; $U = 625$, $n = 25$, $p < 0.001$) than for *P. drouynianus* (1.74 ± 0.19 g, Jalbarragup population). However, for *P. drouynianus* there was also a difference in seed mass between nearby populations (~15 km), with seeds from the Nannup population significantly heavier (2.30 ± 0.11 g; $t = 3.89$, $p < 0.001$) than seeds from Jalbarragup.

The seed is recalcitrant and germinates several months after it is shed from the plant in summer. In southwestern Australia this coincides with the onset of winter rains. In eastern Australia rainfall is more evenly distributed through the year, but lower-temperature and higher-humidity conditions toward winter are likely to be more suitable for seedling establishment than hotter conditions earlier in the year.

Incubation of seeds at higher temperatures reduces the time to germination. For both species germination is fastest at 35°C and begins later at lower temperatures, being slowest at 15°C (Figure 8.2). However, final germination success is similar at all temperatures. Seed kept at 4°C failed to germinate during the time of the trial but did germinate once it was shifted to room temperature (~20°C). There was no germination requirement for fire-related cues such as heat or smoke in either species.

In natural forest populations, *P. drouynianus* produces major crops of seeds one year after a summer fire (Chalwell and Ladd, 2005). Both male and female plants produce sporophylls on the new shoots arising from the lignotuber. Plants that are partially burnt only produce sporophylls on new shoots, with none on any surviving unburnt stems. In the second year after fire sporophyll production is less prolific and seed is rarely produced, and three years or more after fire no sporophylls occur. However, there is no

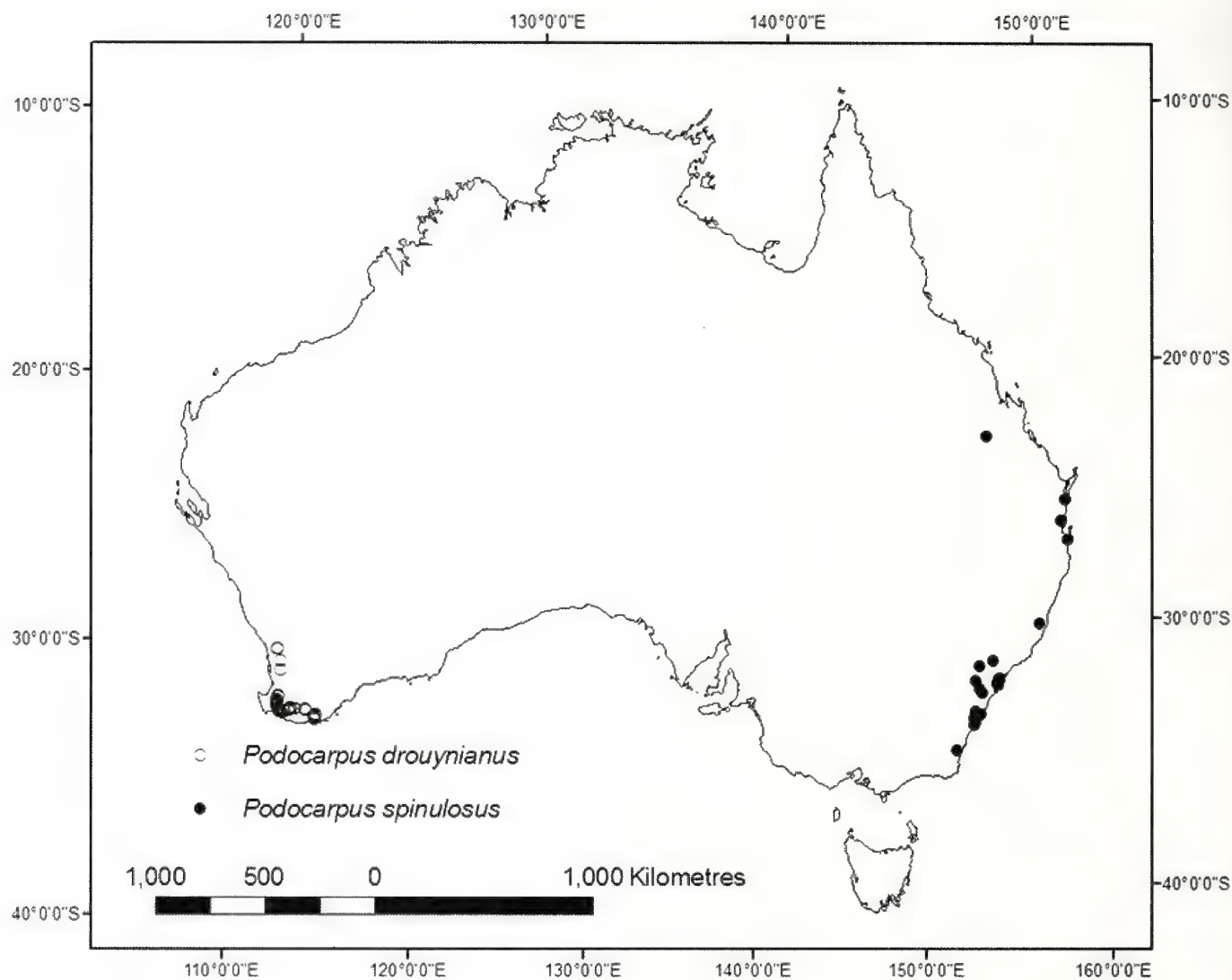


FIGURE 8.1. Map showing the location of records for *Podocarpus spinulosus* and *P. drouynianus*.

TABLE 8.2. Bioclimatic details of *Podocarpus drouynianus* and *P. spinulosus*. Abbreviations: MWU, Mann Whitney U test; NS, not significant. Values in parentheses are the standard error of the mean.

Climatic measure	<i>P. drouynianus</i> (<i>n</i> = 46)	<i>P. spinulosus</i> (<i>n</i> = 22)	Significance
Mean annual rainfall (mm)	1,039 (26)	1,115 (59)	NS
Mean annual temperature (°C)	15.6 (0.1)	17.3 (0.1)	MWU = 893, <i>p</i> < 0.001
Mean precipitation, warmest quarter (mm)	73 (3)	375 (26)	MWU = 1,012, <i>p</i> < 0.001
Mean precipitation, coolest quarter (mm)	478 (13)	231 (70)	<i>t</i> test, <i>p</i> < 0.001

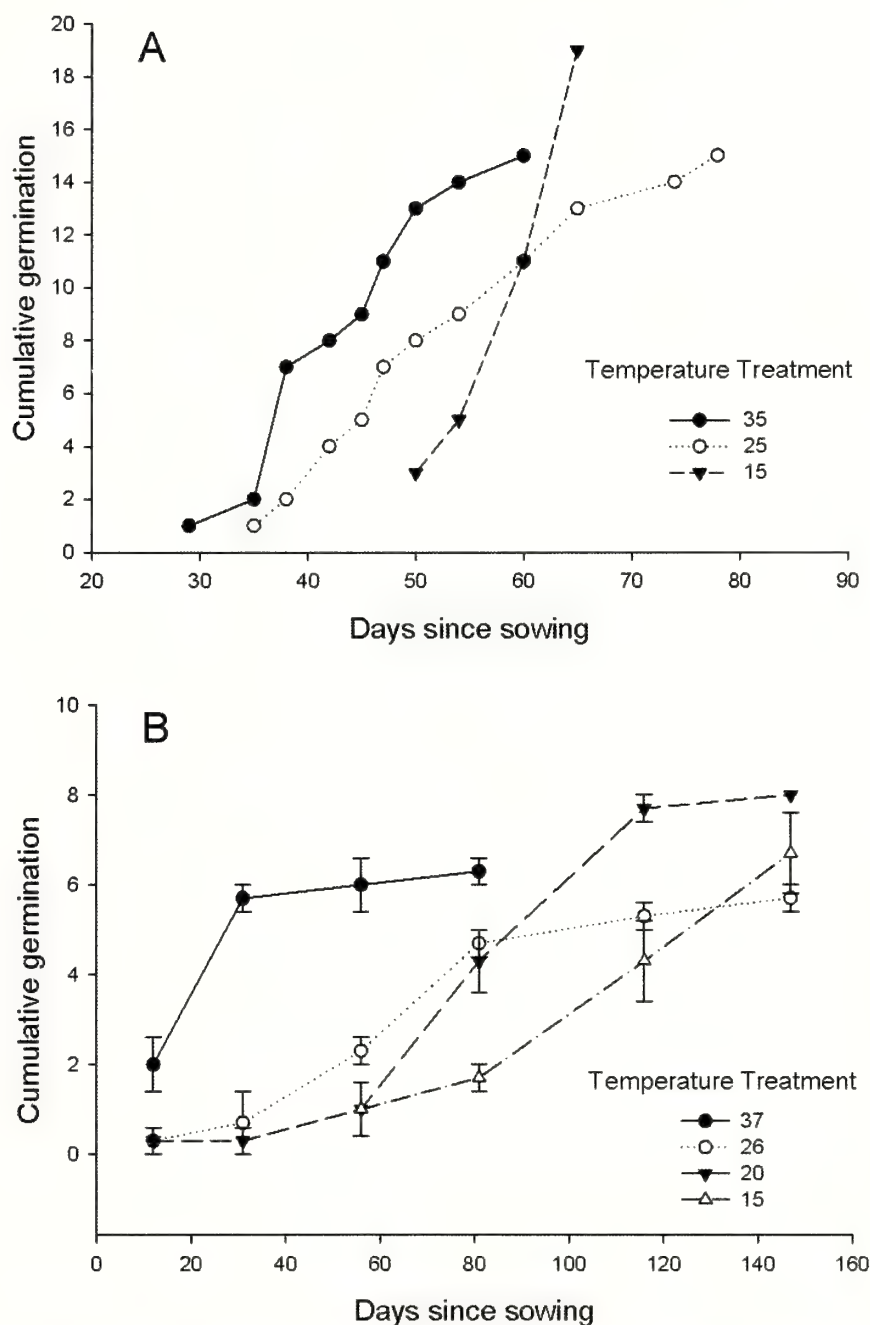


FIGURE 8.2. Seed germination at various temperatures for (A) *P. drouynianus* and (B) *P. spinulosus*. Bars are standard error of the mean ($n = 4$).

simple obligate relationship between fire, new shoots, and seed production as plants that have persisted for many years without fire in paddocks after forest clearing may produce seeds on the new growth from established stems. Thus, the reproductive response to fire appears to break down if aboveground stems grow undisturbed by fire for

long intervals. Seed production of *P. spinulosus* in natural populations has not been followed for sequential years after a fire. However, circumstantial evidence suggests that *P. spinulosus* produces sporophylls in most years. A population assessed at Pearl Beach two years after a fire was producing copious seed, and plants grown from this seed

in cultivation produced sporophylls each year once plants were 10 years old. Experimentally burnt cultivated plants did not produce sporophylls until two years after the fire. Occasional seeds were also observed on long-unburnt individuals in the Sydney Botanical Gardens. Thus, fire stimulates seed production in *P. drouynianus*, but it is not clear if this is true for *P. spinulosus*.

The transition from ovules to seeds was examined on randomly selected large plants (>30 stems >1 m tall) of *P. drouynianus* at Sawyers Valley, near Perth, in 2004 and 2005. Mean ovule production in 2004 was approximately 10 ovules per stem (3.9 seeds per stem), whereas in the following year the same stems produced only a mean of 0.8 ovules and no seed was matured (Figure 8.3).

Randomly selected plants at Jalbarragup had a mean of 0.43 seeds m^{-2} , whereas at Sawyers Valley mean seed production from three 100 m^2 quadrats was 0.58 m^{-2} in 1994 but only 0.10 m^{-2} following a patchy fuel reduction burn at the site in 2004 (Figure 8.3). At both sites the 95% confidence intervals were large, indicating high variability of seed production among plants.

At Jalbarragup only eight seedlings were produced from 6,652 seeds that were followed for six months from seed fall (Chalwell, 1994). In a 1998 census of seedlings at Sawyers Valley, establishment was patchy, with 19 seedlings growing from the 1994 seed event in one 100 m^2 plot but no seedlings in the two other plots. Seeds are eaten by emus, parrots, and mammals (including rodents and possums) but depend mainly on emus for dispersal. The passage of podocarp seeds through the gut of the emu has no effect on germinability (Chalwell, 1994). However, the concentration of seeds in emu droppings provides a focus for mammal predation on the seed, especially if feces are deposited in the open in burnt areas, where most are destroyed by secondary predation (Chalwell, 1994).

VEGETATIVE GROWTH AND REGROWTH AFTER FIRE

Seedlings of *P. spinulosus* and *P. drouynianus* begin development of a lignotuber very soon after germination. A swelling mass of stem tissue, and soon afterward buds, begins to develop in the axils of the cotyledons in both species (Figure 8.4a,b). In *P. drouynianus* cotyledonary axillary buds appear within three months of the plumule emerging from between the cotyledons. In *P. spinulosus* lignotuber development is slower, with development of a swelling at the cotyledonary node taking up to 22 months. In both species, the swelling expands and shoots are produced within five months. In *P. spinulosus* there may be asymmetrical development of the lignotuber

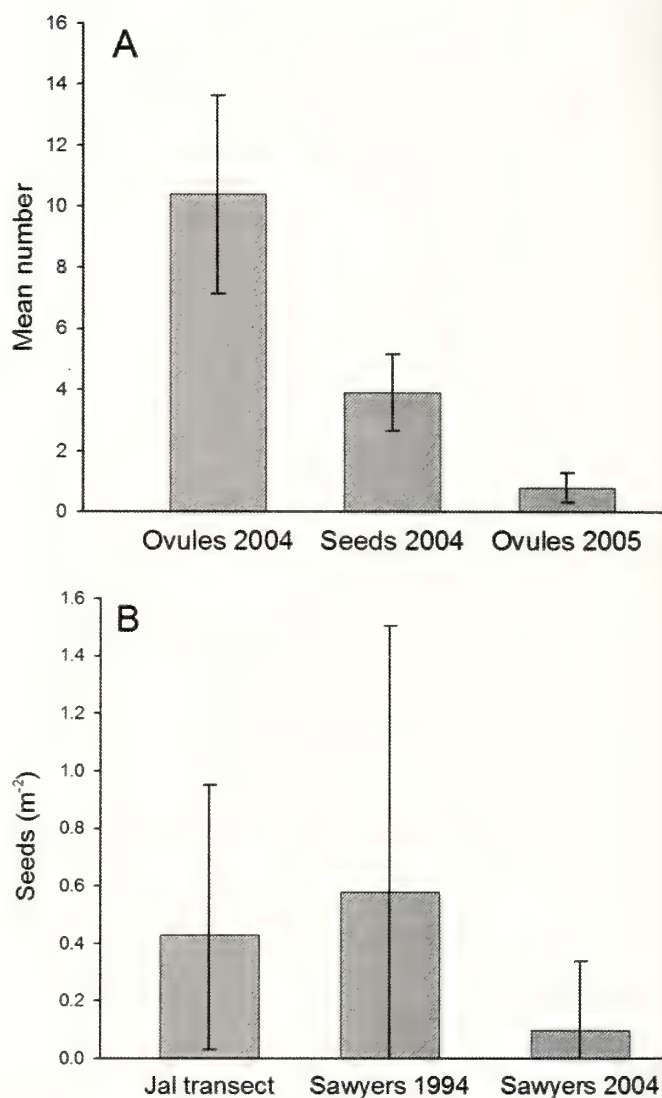


FIGURE 8.3. Reproduction in *Podocarpus drouynianus*, showing (A) ovules and seeds from marked plants over two years, produced after a fire at Sawyers Valley, east of Perth, in 2003; (B) seed production (seeds m^{-2}) from plants on a transect at Jalbarragup (Jal, south of Perth) after a fire in 1993 and from 100 m^2 quadrats at Sawyers Valley after fires in two different years (1993 and 2003). Bars are 95% confidence intervals.

with expansion on the lower side if the stem is bent, until the swelling contacts the soil. The lignotubers of these podocarps have more obvious buds than seen in lignotubers on most other Australian species. The lignotuber of *P. drouynianus* develops by extending lobes downward into the soil. With time, the underground structure may branch (Figure 8.4c), and in older plants the extent of the genet may be >1 m long (Figure 8.5f).

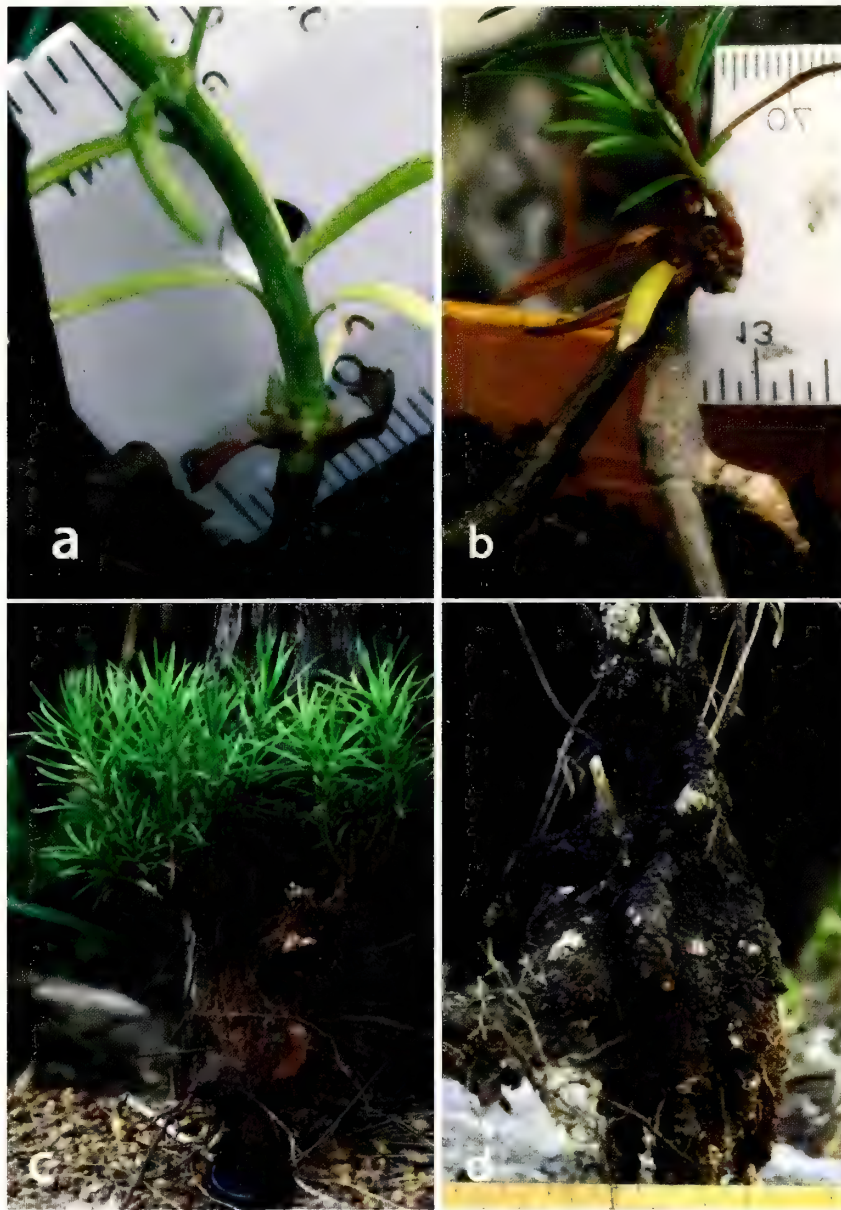


FIGURE 8.4. Lignotubers of *Podocarpus*, showing (a) very young lignotuber buds in the cotyledon axils of *P. drouynianus* (lower scale in mm); (b) new shoot on a young stem burl of *P. spinulosus* (upper scale in mm); (c) excavated adult plant of *P. drouynianus*; (d) lignotuber of *P. drouynianus* for a plant approximately seven years old (scale in cm).

Lignotubers develop quickly in both species. In cultivated *P. spinulosus*, six-year-old plants that were burnt produced new shoots from the lignotuber. Although it is not known how old the lignotuber of *P. drouynianus* needs to be before it can survive fire, its faster early development (described above) suggests that juveniles may become tolerant to fire even more quickly.

Swellings may develop in higher leaf axils of *P. spinulosus* (Lacey and Johnson, 1990) and may also occur along the stems in mature plants (Figure 8.5a), usually with a geotropic development. Although they are not in the position of a lignotuber, they are identical to the lignotuber in their morphology and bud development. There may be many outgrowths on arching stems, and if these

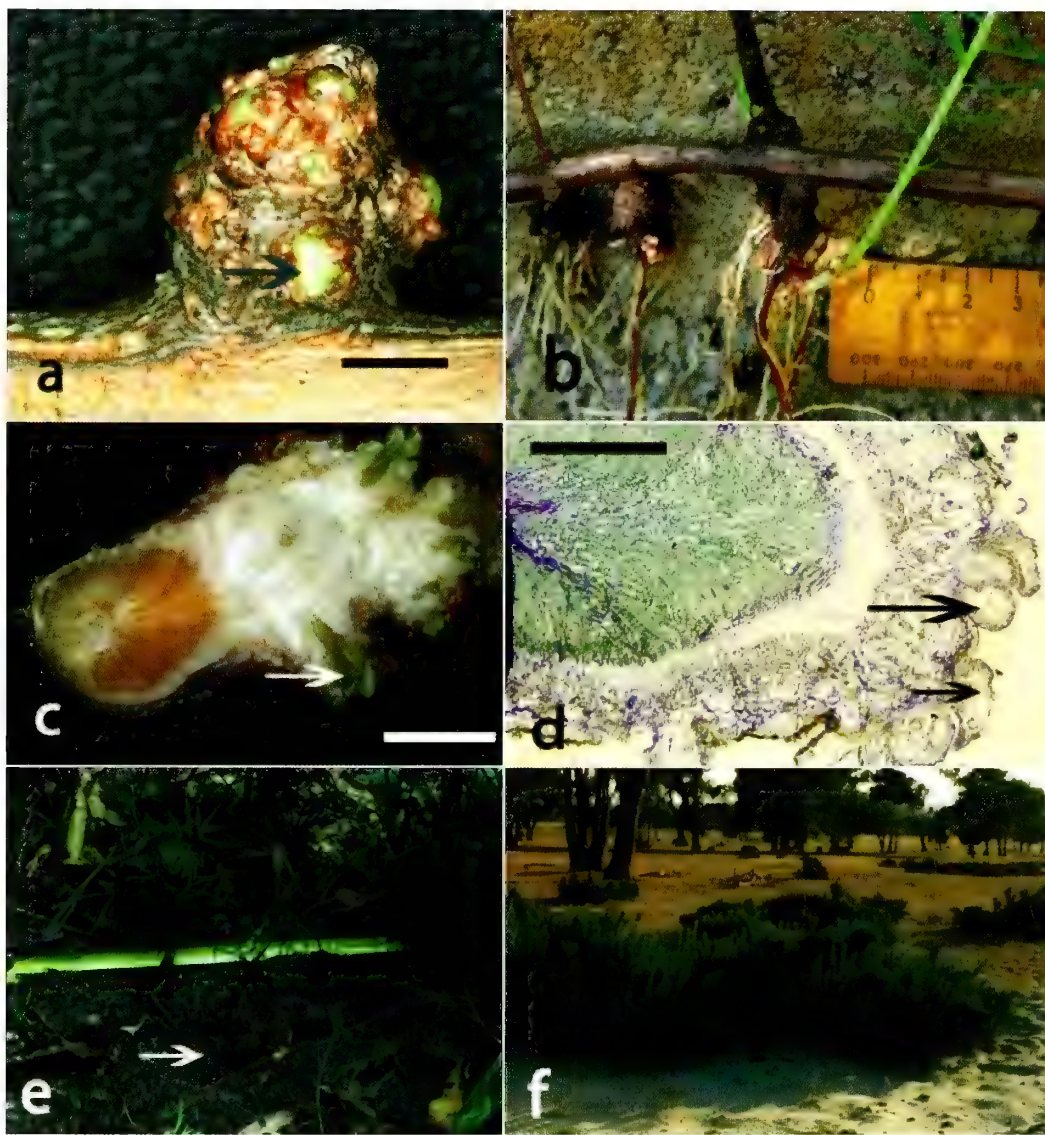


FIGURE 8.5. *Podocarpus* stem structures and growth form, showing (a) a young stem burl of *P. spinulosus*, with the arrow pointing to a bud apex covered by a bract (scale bar = 2 mm); (b) shoots and roots growing from a *P. spinulosus* stem burl that had been buried in the soil, with a large shoot originating below many of the roots (scale bar in cm); (c) transverse hand section of a stem burl of *P. spinulosus*, with the arrow pointing to a bud apex (scale bar = 10 mm); (d) light micrograph of a transverse section through a *P. spinulosus* stem burl, with the arrows pointing to bud scales (scale bar = 0.5 mm); (e) excavated prostrate stems (arrow) of *P. spinulosus*, showing shoots produced from a number of stem burls; (f) clumps of *P. drouynianus* in cleared vegetation, with each clump likely to be a genet.

touch the ground, roots develop from the base of the structure. If the stem is severed from the parent plant or burnt, shoots are produced, and an independent plant develops. The fate of the buds on the stem swelling is undetermined, and buds may develop into roots or shoots. Shoots may develop distally from roots but then grow upward (Figure

8.5b). Sections through a young stem swelling show that the xylem grows out from the main axis of the stem (Figure 8.5c), but the buds on the surface of the swelling develop in proliferated cortical tissue (Figure 8.5d) and have a vascular trace extending through the xylem of the stem toward what was the primary stem tissue as the initial

stem developed. As the stem swellings increase in size, they develop a woody core and seem to be a condensed and thickened shoot with abundant superficial buds that can develop into roots or shoots.

Adult leaves of both *P. spinulosus* (length 5.7 ± 0.1 cm, width 3.4 ± 0.1 mm, length:width ratio 16.9 ± 0.4) and *P. drouynianus* (length 8.2 ± 0.3 cm, width 3.4 ± 0.1 mm, length:width ratio 24.5 ± 1.1) are significantly narrower (Kruskal Wallis test, $p < 0.001$) and have a significantly greater length:width ratio (Kruskal Wallis test, $p < 0.001$) than the mean for other species in the subgenus *Foliolatus* (length 8.8 ± 1.1 cm, width 10.1 ± 1.1 mm, length:width ratio 9.1 ± 0.9).

POPULATION STRUCTURE

The few populations of *P. spinulosus* that have been measured contain more small plants than occur in *P. drouynianus* populations (Figure 8.6). Of the four populations measured at three sites, three had a relatively high proportion of plants in the smallest size class (Crommelin 4 is the exception, Figure 8.6B). In addition, there were few individuals with lignotubers >50 cm in circumference, whereas *P. drouynianus* populations had a much higher proportion of large individuals.

Only two population structures are shown for *P. drouynianus* (Figure 8.6C), although others are presented in Chalwell and Ladd (2005). The plants of this species generally grow much larger than those of *P. spinulosus*. Plot data from Sawyers Valley (sampled in 2003) show a high proportion of small (young) individuals, reflecting survival of recruited seedlings after a fire in 1994. In this species the population structure (ignoring seedlings recruited after the last fire) approximates a normal curve, although skewed to smaller individuals in the Jalbarragup and larger individuals in the Sawyers Valley populations (Figure 8.7), respectively.

The population structure of *P. spinulosus* is difficult to interpret in terms of recruitment of new genets to the population. Plant stems tend to be low and spreading in contrast to the upright growth of *P. drouynianus*, so that ramet proliferation by layering may be common. In the Pearl Beach Crommelin 1 population (Figure 8.6B) many apparent individuals were suckers from procumbent stems, either from stem burls or from parts of the stem without swellings (Figure 8.5e). Pearl Beach Crommelin 4 plants were generally larger. The Yalwal population seemed to consist mostly of shoots produced from stem swellings that had touched the ground and produced roots and shoots; most had only one or two shoots (Figure

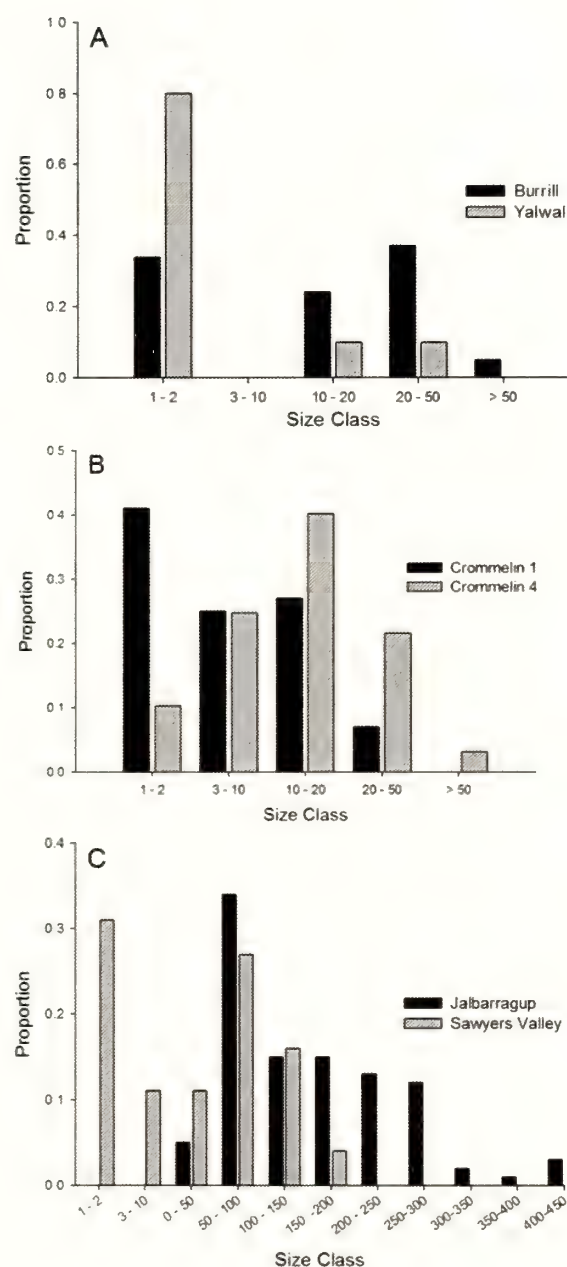


FIGURE 8.6. Size class structures for populations of *Podocarpus drouynianus* in southwestern Australia and *P. spinulosus* in eastern Australia. The first two classes are shoots per plant, and the subsequent categories are the circumference of the lignotuber. (A) *Podocarpus spinulosus* population at Burrill Lake (plot size 100 m², measured 14 July 1994) and at Yalwal (plot size 100 m², measured 15 July 1994); (B) *P. spinulosus* population at Crommelin Reserve, Pearl Beach (quadrat sizes: site 1 = 30 m², site 4 = 10 m²; measured 22 January 1994); (C) *P. drouynianus* population at Sawyers Valley (plot size 100 m², measured on 30 December 2003) and at Jalbarragup (measured January 1994, plants enumerated from 15 plots totaling 375 m²).



FIGURE 8.7. Sawyers Valley population of *P. drouynianus*, showing the size of the plants to 1.5 m in the understory of the *Eucalyptus marginata* open forest (photo by B. L. Turner).

8.6A). It was not possible to determine the original number of genets in this population.

DISCUSSION

Podocarpus spinulosus and *P. drouynianus* are both in the subgenus *Foliolatus* and are phylogenetically closely related to each other but relatively distant from the rest of the species in the genus (Conran et al., 2000; Biffin et al., this volume). Although there is abundant evidence of podocarps in the Australian fossil record, there is no evidence of podocarps in dry environments. Analyses by Brodribb and Hill (1998) concluded that modern podocarp distribution was constrained by seasonal drought, with species largely confined to moist, aseasonal or weakly seasonal climates. The occurrence of these two species on the opposite sides of the Australian continent and their adaptation to fire-prone, moderately to strongly seasonal environments that cannot have been in contact for at least 20 million years suggest early evolution of the fire-tolerant life-form in *Podocarpus* and a long history of stasis in the species. It seems more likely that these two species are a result of vicariant speciation rather than the result of long-distance dispersal.

In Australia there has been radiation of a number of angiosperm groups concomitant with the drying of the continent through the Tertiary. However, in many cases only a small number of genera within a group (such as a family) have developed the required attributes to allow persistence under conditions more arid than those under which the parental group evolved. The groups that achieved arid adaptive changes have become spectacularly successful in speciation, whereas their generic relatives in the rainforest are usually species poor (e.g., Proteaceae; Johnson and Briggs, 1981; Jordan et al., 2008). Groups that are principally represented in rainforests but have a few species in dry forests are less common. In Australia the family Meliaceae may be an example, with *Synoum* common in some eucalypt forests of the east coast but the majority of genera found in rainforests of Australia or overseas. However, *Podocarpus* fits into this category, with the two southern Australian species the only ones to make an evolutionary excursion into drier forests. To do this, they had to undergo a number of morphological changes in their typical podocarp plant form.

Both species have narrower leaves and a much greater length to width ratio than the mean dimensions for other species in the subgenus *Foliolatus*. In the podocarps (and conifers in general), water is distributed from the main leaf

vein to the photosynthetic tissue via tracheids in accessory transfusion tissue rather than from a ramified network of veins as in angiosperms. This seems to be a less-efficient water distribution system than a network of veins. Under drought stress it has been shown that the tracheids of the accessory transfusion tissue in *P. grayi*, a rainforest species with broad leaves, collapse and therefore cease to transfer water to the mesophyll cells (Brodribb and Holbrook, 2005). The narrow leaves of *P. spinulosus* and *P. drouynianus* ensure there is only a short distance to transport water to the mesophyll from the primary leaf vein, which benefits the plant in terms of drought resistance. Brodribb and Hill (1998) showed that *P. drouynianus* had the greatest water use efficiency when compared to the other 12 species studied, five of which were podocarps from areas with greater than 1,500 mm rainfall per annum.

Both fire-tolerant podocarp species have retained their ancestral reproductive characteristics of dioecy, wind pollination, vertebrate dispersal, and recalcitrant seed germination. *Podocarpus drouynianus* has retained a form of synchronized cone formation and seeding, which occurs in at least some other podocarps (Geldenhuys, 1993), but this is cued by fire rather than other environmental signals. The benefits of this equate to masting and include increased effectiveness in a wind-pollinated species (Smith et al., 1990), seed predator satiation (Donaldson, 1993), and increased propagule visibility for a species that relies on animals for seed dispersal. Pyrogenic reproduction in *P. drouynianus* makes it a member of a relatively small group of Australian woody and herbaceous plants that flower almost exclusively in the first year or first few years after fire (Burrows and Wardell-Johnson, 2003); these include *Angophora hispida* (Auld, 1986), *Doryanthes excelsa*, *Telopea speciosissima* (Denham and Auld, 2002), and the wind-pollinated *Stirlingia latifolia* (Ladd and Wooller, 1997). *Podocarpus drouynianus* has likely been constrained to this reproductive solution in a fire-prone environment by its ancestral characteristics, including the absence of a cone structure for on-plant seed storage and having a seed too large to survive in the soil seed bank. Seed maturity of *P. drouynianus* occurs in winter (following dispersal in late summer), allowing germination at a time when conditions are most likely to be reliably moist in the Mediterranean-type climate of southwestern Australia. The embryo in the seed is immature when the podocarpium is "ripe" (i.e., fully colored) and continues to grow when the seed is initially dispersed. The more rapid germination with increased incubation temperature indicates that the rate of embryo development increased with higher temperature, so the embryo matured and forced its

way out of the seed coat earlier than in seeds incubated at lower temperature.

Animal dispersal is common in podocarps, although it is not universal (Nanami et al., 1999). Geldenhuys (1993) identified birds and bats as important dispersers of South African podocarp seed, and this certainly occurs in a number of New Zealand podocarps (Ogden and Stewart, 1995). The emu is the most important disperser of *P. drouynianus*; other animals may move the seed, primarily as predators rather than dispersers. The emu is a large and wide-ranging bird. It consumes gravel that lodges in the gizzard, where it serves to grind food. However, seeds of many species pass the digestive tract unharmed and may take from 3 to 50 hours to pass through (Davies, 2002). In this time an emu may traverse several kilometers, so podocarp seeds may be deposited in feces far from the location where they were consumed. The large seed size (in the upper range of seed sizes in southwestern Australian plants) should allow seedlings to establish even in unburnt vegetation and, after a subsequent fire, to resprout in the relatively competition-free environment, so long as at least a few years are available for lignotuber development before fire (Chalwell and Ladd, 2005). Nevertheless, most recruitment probably occurs in newly burned areas relatively close to parent plants, and there seedlings have the maximum possible time to establish before fire recurs (i.e., approximately equal to the mean fire interval). The large seed size is still an advantage in an environment where most species have much smaller seeds. There are no records of dispersal of *P. spinulosus* seed, but the propagule structure is similar to *P. drouynianus*, and emus also occur along the east coast of Australia and are likely dispersers. The apparent absence of fire-stimulated fruiting in *P. spinulosus* may indicate that recruitment in this species occurs in unburned sites, but further research is needed on patterns of recruitment in this species.

Adie and Lawes (this volume) highlight podocarp regeneration failure in grassy podocarp forests in South Africa, presumably due to competition between grasses and podocarp seedlings. Western Australian eucalypt forests tend to have a relatively open ground layer, so that postfire competition with podocarp seedlings is not likely to be as severe as in the South African wet forests.

There has been some consideration in this volume of the idea that podocarps tend to occur on nutrient-poor soils. *Podocarpus drouynianus*, in particular, is found on deep sands and old lateritic soils in southwestern Australia that have been considered as among the most nutrient poor in the world and are particularly low in phosphorus (Lambers et al., 2008). *Podocarpus spinulosus* also grows

on impoverished, thin soils over Permian sandstones in eastern Australia, but it may also extend into gullies on colluvial material, where nutrient status would be better because of a relatively high organic content in the soil. However, both species, in common with many other podocarps, survive well on nutrient-poor substrates.

The most obvious innovation in the Australian podocarp species is the ability to resprout from buried stem tissue after fire. This is rare in conifers, being found in only a few species, including *Widdringtonia nodiflora* in South African fynbos (Keeley et al., 1998) and *Actinostrobus acuminatus* in southwestern Australian kwongan (personal observation by the authors), both Cupressaceae. The proliferation of buds at the cotyledonary node is similar to that described for "basal chichi" in *Ginkgo biloba* seedlings (Del Tredici, 1992) and for eucalypts. Although this is not an essential requirement for growing in a fire-prone environment, it does ensure that the plant is resilient to burning over a range of fire frequencies. A few podocarp trees have epicormic sprouts that occur after defoliation by disturbances such as fires (*P. elongatus*; Midgley et al., 1995) or hurricanes, but this is not a particularly widespread trait in conifers (Bellingham et al., 1994). The lignotuber in both species develops in the axils of the cotyledons as in *Eucalyptus* and seems most similar to the "Group C" type of Carr et al. (1984). Del Tredici (1992) described the basal chichi of *Ginkgo*, which seem morphologically similar to the lignotuber of the podocarps and the eucalypts. Basal chichi are considered anatomically identical to the aerial chichi but are considered to develop from a bud, whereas aerial chichi develop in association with wounds to the trunk (Del Tredici, 1992). The aerial stem outgrowths of *P. spinulosus* develop in association with an axillary bud and thus differ ontogenetically from the aerial chichi of *Ginkgo*. However, the aerial chichi of *Ginkgo*, like the *P. spinulosus* form, can produce both shoots and roots. Lacey and Johnson (1990) called the woody outgrowths of *P. spinulosus* as lignotubers, but clearly, ontogenetically they are not strictly equivalent, as lignotubers should originate in association with the cotyledonary node. In terms of overall attributes the term chichi for the *P. spinulosus* stem outgrowths is appropriate.

Podocarpus drouynianus is a strong resprouter after defoliation. However, unlike many other lignotuberous species with which it co-occurs, the bud bank is completely depleted after each fire (Chalwell and Ladd, 2005), so it might not be well served by its bud bank under a regime of increasingly frequent fires, as projected for southwestern Australia as climate becomes hotter and drier (Williams et al., 2009). In *P. drouynianus* the root stock/lignotuber

may produce short lateral shoots that lead to a relatively compact plant form with many stems that rarely grow >3 m tall, whereas in *P. spinulosus* the lignotuber tends to be smaller and the stems more spreading. Stems frequently become buried under leaf litter and debris, which allows rooting from the chichi and subsequent shoot development. Initial connection to the parent plant would be beneficial, allowing the ramet to develop even though it may be heavily shaded or covered with litter. However, after fire the connection to the parent may be severed, and the ramet can resprout in the more open, postfire environment. Similar asexual plant expansion is seen in other conifers and is important in their population maintenance (Hayakawa et al., 2004), although these species do not occur in fire-prone environments.

The contrasting growth forms of these two species can be considered similar to the phalanx (*P. drouynianus*) and guerilla (*P. spinulosus*) strategies of clonal growth (Begon et al., 2006). The guerilla strategy is considered to be advantageous in locating resources (light, nutrients) in a patchy environment (de Kroons and Hutchings, 1995), but it has not been considered in relation to fire and the trade-off between sexual and asexual reproduction. The guerilla strategy can access more sites more quickly than the phalanx strategy, whereas vegetative reproduction may be more secure than sexual reproduction in a fire-prone environment when seedlings have limited fire resistance in the early years of growth. Fire frequency is difficult to summarize for the Australian forests where these species occur and has varied from the Aboriginal period to the present (Abbott, 2003). Indeed, there is considerable controversy about fire frequency in Western Australian forests. It has been deduced that jarrah forest in the Mundaring area (close to Sawyers Valley) could carry a fire every three to five years and that the frequency of fires lit in jarrah forest by Aborigines in summer was two to four years (Abbott, 2003). In contrast, using fire scars on tree stems, Burrows et al. (1995) estimated an average interval between tree-scarring fires of about 80 years before European settlement and about 17 years afterward. However, they suggested that lower-intensity fires of greater frequency might not scar large trees. A fire map in Fox (1999) shows that fire return times for southwestern Australia are about 10 years, whereas for much of the area occupied by *P. spinulosus* fire return times are three to five years and thus equally or more frequent than in Western Australia.

Slower lignotuber development in *P. spinulosus* than in *P. drouynianus* seedlings may be related to the greater ability of guerilla development in the former. The guerilla strategy involves the lax branches contacting the soil and

the chichi structures developing roots to produce ramets that eventually become independent plants. In the Crommelin Reserve the plants censused in site 1 were predominantly of 1–2 shoots and were mostly produced from a network of formerly continuous procumbent stems (covered with plant litter) connecting chichi that had produced roots and a few shoots at sporadic points. A similar situation applied at Yalwal, but at that site the stems were aerial and mostly still intact. This species seems to rely heavily on asexual reproduction to maintain the population, in contrast to *P. drouynianus*, which has a much more compact growth form and can only slowly extend the area occupied by a genet. Colonization of new sites by this species will be mainly dependent on seeds, so strong postfire reproduction (masting) will be beneficial to this species in maintaining population numbers.

In frequently (and predictably) disturbed environments there has been a dichotomous selection for a seeder plant functional trait and refinement of what is often a generalized trait for resprouting. Seeder species need to develop a seed bank in preparation for the next stand-destroying fire, whereas sprouter species rely heavily on vegetative regeneration. The ancestral reproductive trait of podocarps is as a seeder rather than a sprouter. The seeds are large and not contained in fire- or desiccation-resistant cones; they are unsuitable for storage in soil because of their large size and lack of dormancy. Thus, the ancestral podocarp did not have a suitable strategy for surviving in a fire-prone environment. The development of the ability to resprout laid the foundation for the success of *P. drouynianus* and *P. spinulosus*, and the other modifications they display are incremental, not radical. By being able to resprout, *P. drouynianus* can emulate a suite of angiosperms that are cued to reproduce after fire on newly produced stems and thus distribute seeds into a relatively competition-free and nutrient-rich environment. Bellingham and Sparrow (2000) note that there are trade-offs between vegetative resprouting and seeding. The reproductive trade-off for sprouters is that they normally do not produce as many seeds as seeder species. In most podocarps, adult plants produce seeds in all years, although there may be mast years (Geldenhuys, 1993), and they may have a variable but low investment in buds for resprouting. *Podocarpus drouynianus* has an extreme form of masting, with seeds produced only after fire. In years between fires (with fire intervals ranging from 10 to 30 years) the plants can accumulate resources to fuel resprouting and reproduction after the next fire occurs. However, it is unknown whether very long intervals without fire lead to decline in the bud bank and an increased susceptibility to mortality from fire,

as has been described for some other fire-tolerant lignotuberous species (Wellington and Noble, 1985; Enright et al., 1998). Alternatively, the time since the last fire may become so long that some level of annual fruiting commences, as identified for plants in paddocks that have been isolated from fire for many decades. More work is also needed on reproduction in *P. spinulosus* to determine its pattern of seed production in relation to fire.

As predicted by Midgley (1996), the development of resprouting has meant that both *P. drouynianus* and *P. spinulosus* have to relinquish the tall monopodial form characteristic of most podocarps in wet forests. The species have become subdominants in their communities. Nevertheless, they are resilient to both stress (i.e., seasonal drought) and disturbance (i.e., fire), and if persistence at a site is any indication of evolutionary success, *P. drouynianus* has certainly achieved this (as demonstrated in Figure 8.5f), being one of the few native species to survive in the predominantly cleared area. These species clearly represent podocarps “on the edge” in terms of their adaptations to a set of environmental circumstances beyond those associated with any other members of this large, and typically conservative, plant family.

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Conifer–Angiosperm Interactions: Physiological Ecology and Life History

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ABSTRACT. Worldwide, conifers are most successful on sites subject to chronic stresses that limit productivity (low temperatures, nutrient poverty, poor drainage). They are poorly represented in the lowland tropics but are often important in montane tropical forests. Here I explore some functional differences between leaf and xylem traits of conifer and angiosperm trees and their implications for the distributions of these two groups on environmental gradients. Analysis of a global data set shows that compared with angiosperm trees, conifers tend to have longer-lived leaves with greater mass per area (LMA) and lower mass-based photosynthetic capacity. As leaf life span is thought to be the main determinant of nutrient retention time, the prominence of conifers on infertile soils worldwide is at least partly attributable to thrifty use of nutrients through long leaf life spans. Furthermore, because leaf life span correlates with litter decomposition rates, these leaf trait differences could potentially influence the competitive balance between conifers and angiosperms via positive feedbacks on nutrient cycling. Although scaling of leaf life span with LMA is similar in the two groups, angiosperms achieve slightly longer leaf life spans than conifers of similar photosynthetic capacity. This might be caused by less-efficient leaf display in conifers, resulting in the useful life span of leaves being curtailed by self-shading. Representatives of both lineages have narrower conduits in the temperate zone than in the lowland tropics/subtropics, reflecting selection for resistance to freeze-thaw embolism in cold climates. However, conduit diameters of conifers and angiosperm trees differ more in tropical and subtropical forests than at higher latitudes. This probably reflects mechanical constraints on maximum tracheid diameters in the homoxylous wood of conifers, preventing this group from producing the highly conductive wood typical of fast-growing angiosperm pioneers in tropical forests. This pattern might explain why coexistence of conifers and angiosperms is more common in temperate forests and on tropical mountains than in the lowland tropics. Impairment of angiosperm carbon gain by freeze-thaw embolism during cold weather may further narrow performance differences between the two lineages on temperate sites. Differences in canopy residence time probably deserve more attention as a determinant of conifer–angiosperm coexistence in many temperate forests, the longer life span of conifers compensating for infrequent recruitment.

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INTRODUCTION

Conifers were dominant in forests worldwide during the Triassic and Jurassic (Florin, 1963; Miller, 1977) but have since been largely replaced by angiosperm trees in the lowland tropics, as well as losing much ground in temperate forests. Conifer dominance is now restricted mainly to cold or infertile sites (Bond, 1989), although they coexist with angiosperms in a variety of forest types (Enright and Hill, 1995; Becker, 2000). The advance of angiosperms at the expense of conifers and other lineages may have significantly altered ecosystem processes in forests. It has been suggested, controversially, that rainforests as we know them are a product of changes in ecosystem water fluxes resulting from angiosperm innovations in anatomy and physiology (Boyce et al., 2009). Accelerated nutrient cycling is another possible consequence of the angiosperm revolution at the end of the Cretaceous (Berendse and Scheffer, 2009).

Angiosperm success was initially attributed to reproductive innovations (Raven, 1977; Regal, 1977). Biotic pollination, used by many angiosperms, might require less investment in pollen than wind pollination and might be more effective at achieving sexual recombination in low-density populations. Vertebrate seed vectors might have dispersed seeds further and to safer sites. After reviewing fossil and contemporary evidence, Midgley and Bond (1991) concluded there was little support for the reproductive hypothesis. For example, isolated female trees of wind-pollinated *Podocarpus* in South African forests sometimes set appreciable quantities of seed (Midgley, 1989), calling into question the supposed inefficiency of wind pollination in dense, species-rich forests. Furthermore, vertebrate-dispersed fruits, far from being a uniquely angiosperm innovation, are also found in many conifers such as *Taxus*, *Podocarpus*, and *Dacrydium*.

In contrast, Bond (1989) argued that the outcome of competition between angiosperms and conifers could be determined during the juvenile phase, as a result of vegetative differences between these two groups. Tracheids, being limited to relatively small diameters, are usually less conductive than angiosperm vessels. This is likely to limit the ability of conifer seedlings to supply leaves with water and hence constrain carbon gain and growth. Bond (1989) further contended that very small initial leaf areas restrict the growth rates of young conifer seedlings; although some conifers can attain high productivity in later life by accumulating many leaf cohorts, their seedlings are likely to be outcompeted by angiosperms on productive sites that permit rapid growth. The more sophisticated vascularization

of angiosperm leaves also enables them to produce a wider variety of leaf sizes and shapes (Bond, 1989), giving them advantages in light interception efficiency (C. H. Lusk, unpublished data). Bond (1989) famously applied the “tortoise and hare” metaphor to competition between conifers and angiosperms. In essence, conifers are relegated mainly to cold or infertile sites because these adverse environments nullify or reduce the potential growth advantages of the angiosperm “hares,” preventing them from outpacing the “tortoises.”

Bond’s landmark paper is first and foremost a synthesis of ideas, and relatively few data were then available to test or explore the mechanisms involved. The intervening 20 years have witnessed tremendous growth of plant physiological ecology; although only a handful of empirical papers have directly addressed the issue of conifer-angiosperm interactions (e.g., Becker et al., 1999; Lusk et al., 2003; Brodribb et al., 2005), a good deal of relevant data and ideas have nevertheless been published. Although both lineages encompass a wide range of maximum growth rates, comparative studies of seedlings confirm that even relatively “harelike” conifers such as *Pinus* species are unable to match the performance of the fastest-growing early successional angiosperm trees (e.g., Cornelissen et al., 1996; Reich et al., 1998). Differences between maximum seedling growth rates of late successional conifers and angiosperms have also been reported in some studies (e.g., Hattenschwiler and Körner, 2000) but not in others (e.g., Shipley, 2002), suggesting that some angiosperms are also rather “tortoiselike.”

Developments in plant physiological ecology have also given us a better understanding of the traits underlying variation in plant growth and survival in different habitats (e.g., Lambers et al., 1998). Of particular relevance here is our increased understanding of the traits that enable conifers to dominate many forests on cold or infertile sites despite slow seedling growth rates (Sperry et al., 2006). This chapter examines data on some stem and leaf traits relevant to carbon gain and growth of juvenile conifers and angiosperms and, therefore, likely to influence the outcome of competition between them. I also briefly consider evidence that differences in adult longevity contribute to the coexistence of conifers and angiosperms in some temperate forests.

CONDUIT DIAMETERS

It has long been recognized that vessels tend to be more conductive than tracheids, as their diameters are

usually larger (Zimmerman and Brown, 1971). According to the Hagen-Poiseuille law, conductivity of a conduit is proportional to the fourth power of its diameter. All else being equal, a conduit with a diameter of 60 μm should thus conduct about 16 times more water than one with a 30 μm diameter.

More recently, there has been a better understanding of the trade-offs associated with variation in xylem anatomy and how small conduits can be advantageous in certain situations. Conduit diameter is strongly correlated with susceptibility to freeze-thaw embolism (Davis et al., 1999). When xylem sap freezes, air bubbles form inside conduits; when the ice thaws, these bubbles can either dissolve back into the sap solution or expand to fill the entire conduit, blocking water transport to the subtended leaves. There is less risk of freeze-thaw cavitation in small conduits because the bubbles formed therein are small and easily redissolved during thawing, unless xylem tensions are very high (Hammel, 1967; Feild and Brodribb, 2001). As a result, species with narrow conduits suffer much less loss of hydraulic conductivity after freeze-thaw events. This is probably one of the main factors underlying the prominence of conifers in cold climates worldwide.

Some angiosperms in tropical forests have very large vessel diameters (e.g., Ewers et al., 1990). This presumably reflects a lack of selection for resistance to freeze-thaw embolism in tropical climates and the advantages of heteroxylous wood: as fibers do most of the job of supporting the tree's weight, vessel diameters are not subject to strong mechanical constraints. On the other hand, the dual role of tracheids in homoxylous wood probably means that conifers are not as well placed to take advantage of the relaxed climatic constraints on conduit diameters in the tropics. Wood made up of very large diameter tracheids would have a very low density and so might be too weak to support a large tree. Tracheid dimensions may thus be limited more by unicellularity and their structural role than by the need to protect against cavitation (Sperry et al., 2006).

If constraints on conduit diameters differ between conifers and angiosperms, this points to one possible explanation for the scarcity of conifers in the lowland tropics. On sites subject to freezing temperatures during the growing season (e.g., temperate maritime climates, tropical mountains), angiosperm vessels will likely be constrained to relatively small diameters, not too different from those of tracheids. On frost-free sites, in contrast, angiosperms could potentially develop vessel diameters far in excess of anything achievable by plants with homoxylous wood, giving them a considerable advantage over conifers in terms of stem conductivity (Sperry et al., 2006). This will

influence the economics of hydraulic supply to leaves: for a given investment in stem tissue, angiosperms will be able to irrigate a larger leaf area and/or develop higher leaf conductances, permitting higher potential carbon gain and growth.

Data collated from the literature support the proposal that conifer and angiosperm conduit diameters differ most at low latitudes (Figure 9.1). Reported conduit diameters of evergreen conifers and angiosperms were compared at high versus low latitudes. As data on lowland tropical conifers were scarce, the low-latitude category was broadened to include data from lowland subtropical sites ($<30^\circ$ latitude). Conifers growing at >2000 m elevation in the montane tropics were excluded, as were vesselless angiosperms. Conifer and angiosperm conduit diameters differed only about twofold on average at $>30^\circ$ latitude, and the range of diameters overlapped considerably between the two lineages. In the lowland tropics and subtropics, conifer and angiosperm conduits differed more than fourfold on average, and there was minimal overlap between the two lineages (Figure 9.1). In the tropics, conifers will therefore be at an overwhelming disadvantage in terms of maximum stem conductivity. This is one obstacle to the evolution of fast-growing early successional conifers capable of competing with tropical angiosperms such as *Cecropia* and *Macaranga* (Lusk, 2008). Most conifer species in the lowland tropics are shade-tolerant podocarps, which although never dominant on productive sites, are able to persist in competition with angiosperms by harvesting understory light efficiently (see Brodribb, this volume).

In temperate regions, any angiosperm advantage in stem conductivity will be reduced as the smaller difference in conduit diameters will be compensated to some extent by the high conduit density of homoxylous conifer wood (Sperry et al., 2006). This is one factor contributing to the frequent coexistence of conifers and angiosperms in temperate evergreen forests, although even within this biome, conifer distributions tend to favor relatively cold and/or infertile sites (Enright and Hill, 1995). Even though co-occurring evergreen conifers and angiosperms tend to differ in maximum hydraulic capacity (Feild and Brodribb, 2001; Lusk et al., 2007), this difference will not necessarily translate into higher net carbon gain under all conditions. Feild and Brodribb (2001) found that vessel-bearing angiosperms growing at the timberline in Tasmania were severely affected by freeze-thaw embolism, losing 17%–83% of stem conductivity after a single freeze-thaw cycle. In contrast, none of their coniferous associates lost more than 12% of stem conductivity, as was also true of the vesselless angiosperm *Tasmannia lanceolata*. Even if

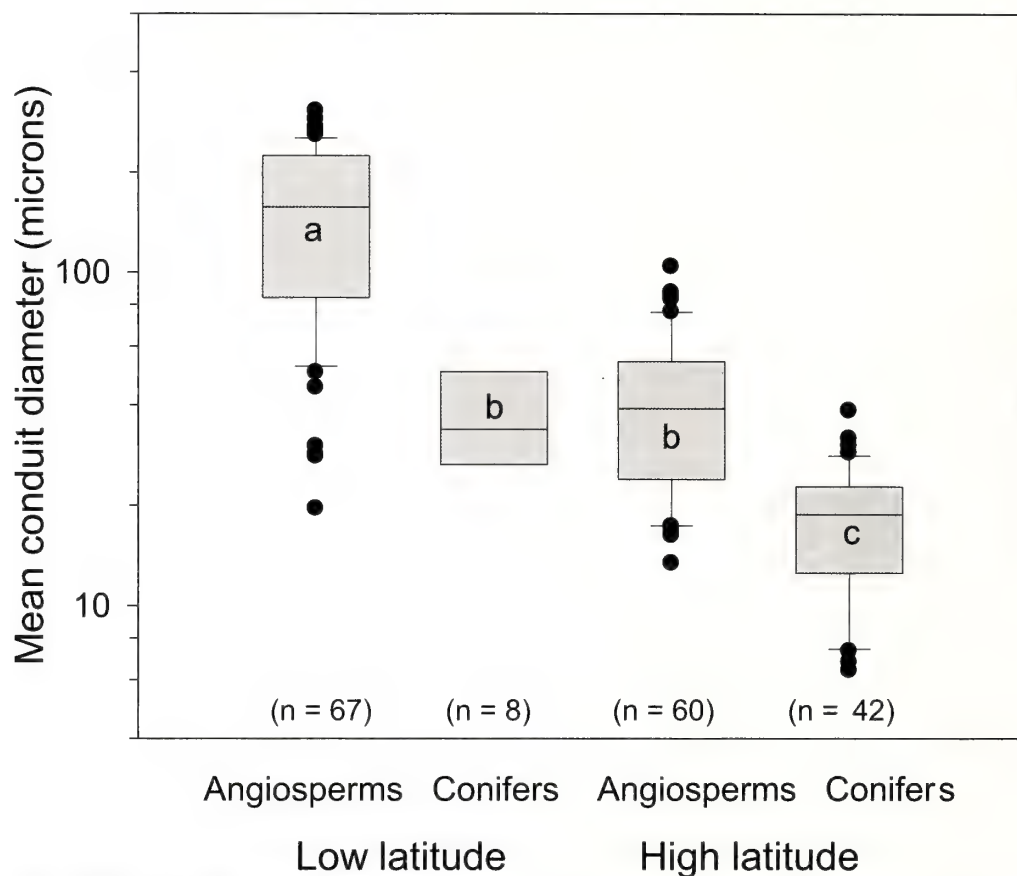


FIGURE 9.1. Conduit diameters of aboveground material from evergreen angiosperms and conifers growing at low latitude ($<30^\circ$) and high latitude ($>30^\circ$). Data are taken from sources in the appendix. Box plots show the 10th, 25th, 50th, 75th, and 90th percentiles. Species growing at high elevations ($>2,000$ m above sea level) were excluded from the low-latitude categories. Values in parentheses show the number of species in each category. Means of categories sharing the same letter do not differ significantly at $p = 0.05$ (Tukey–Kramer honestly significant difference tests). Diameter data were collated by searching BIOSIS previews, obtaining a total of 233 entries from 54 references, representing 166 species. Multiple entries for a species were averaged. Stem diameters in which conduits were measured ranged from 1 to $>1,000$ mm, indicating that the means presented above include unquantified effects of stem diameter on conduit taper.

temperate evergreen angiosperms gain much more carbon than their coniferous associates during frost-free periods, this could conceivably be reversed during winter, when vessel-bearing angiosperms are likely to be partly embolized much of the time.

LEAF TRAITS

Recent reviews have highlighted coordinated scaling of a suite of structural and functional traits of leaves across species and ecosystems (Reich et al., 1999; Wright

et al., 2004). Most leaves worldwide can be ordinated on a single axis of trait variation, reflecting a trade-off between persistence and performance. It must be stressed that this “leaf economics spectrum” represents a general principle of leaf evolution, not a unique law, because the exact nature of bivariate relationships among the traits involved varies geographically (Wright et al., 2005), depending on climate, soils, and which resources are most limiting to plants. It might be asked whether habitat partitioning between conifers and angiosperms reflects different trait-scaling relationships in these two groups (Lusk et al., 2003). For example, conifer leaves have a reputation for

longevity (Chabot and Hicks, 1982; Lusk, 2001): does this reflect an ability to achieve longer life spans for a given investment in leaf mass per area (LMA), and might this explain the success of conifers on nutrient-poor soils? Or does the slope of the relationship between LMA and leaf life span differ between conifers and angiosperms?

A global data set (Wright et al., 2004) was used to compare scaling of leaf life span with LMA in conifers and angiosperm trees. The two groups showed no significant difference in the slope of this relationship or in its elevation (Figure 9.2). Despite differences in leaf anatomy, the two groups achieved similar leaf life spans for a given investment of dry matter in leaf tissue per unit area. However, there was a significant shift along the common slope of this relationship: notwithstanding considerable overlap, extant conifer and angiosperm trees are essentially specialized on different regions of the continuum of leaf life spans. Conifers live up to their “tortoise” epithet by mainly occupying the “slow” end, with most having leaf life spans of >2 years. As leaf life span is the strongest

influence on variation in nutrient residence time in woody plants (Escudero et al., 1992), the prominence of conifers on poor soils in many regions (Escudero et al., 1992; Read, 1995; Burns and Leathwick, 1996; Lusk and Matus, 2000) is therefore at least partly attributable to thrifty use of nutrients through long leaf life spans. Angiosperm trees are concentrated in the middle region of the spectrum, with most, but by no means all, species holding their leaves for between 4 months and 2 years. The “fast” end of the spectrum is dominated by herbaceous plants.

It was also found that the relationship between photosynthetic capacity and leaf life span differs significantly between angiosperms and conifers (Figure 9.3). The slope was very similar in the two groups, although angiosperms leaves achieved slightly longer life spans at a given photosynthetic capacity. One possible explanation lies in the

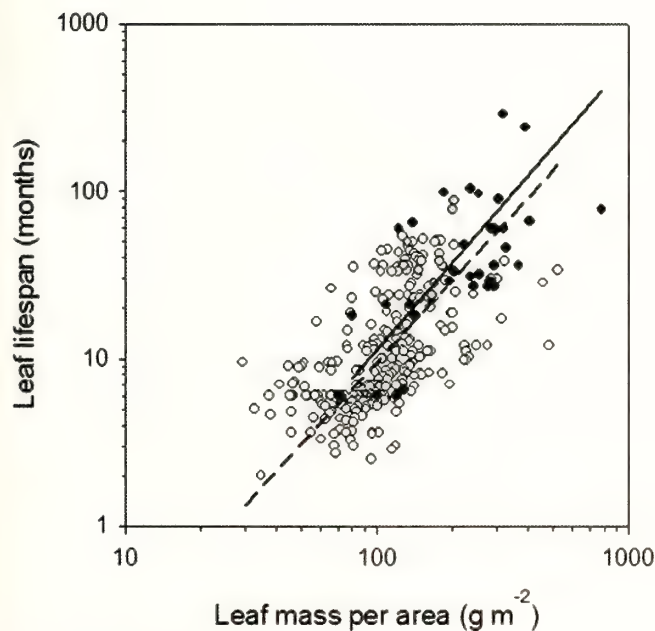


FIGURE 9.2. Relationships of leaf life span with leaf mass per area of evergreen angiosperms (white circles, dashed line) and conifers (solid line; gray circles show podocarps, and black circles represent all other conifers). Major axis tests (Falster et al., 2006) showed no difference in slope or elevation but showed a shift along a common slope ($p < 0.0001$). Data are from Wright et al. (2004).

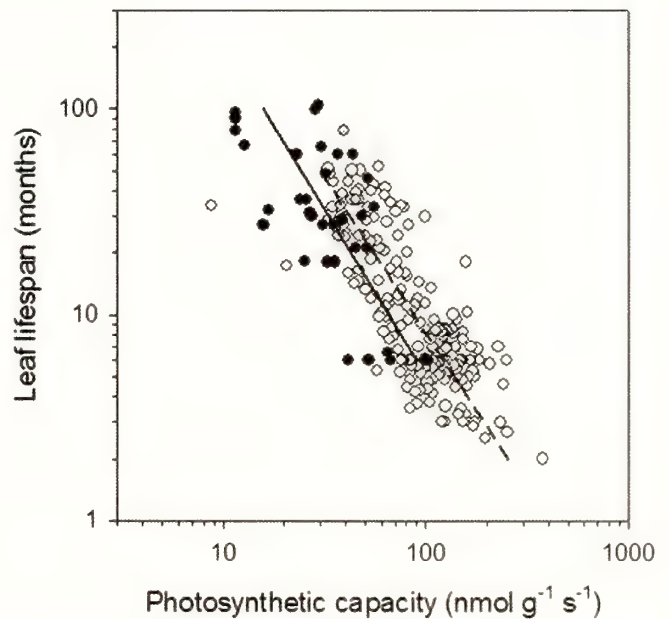


FIGURE 9.3. Relationships of leaf life span with photosynthetic capacity of evergreen angiosperms (white circles, dashed line) and conifers (solid line; gray circles show podocarps, and black circles represent all other conifers). Major axis tests (Falster et al., 2006) showed no difference in slope but showed a significant difference in elevation ($p = 0.003$) as well as a shift along a common slope ($p < 0.0001$). Angiosperm leaves therefore had significantly higher photosynthetic capacity, on average, than conifers, as well as living longer than conifer leaves of comparable photosynthetic capacity. Data are from Wright et al. (2004).

fact that large-leaved angiosperms often have more efficient leaf display than conifers (C. H. Lusk, unpublished data); the resulting differences in self-shading may influence the useful life span of leaves.

In view of the subject of this book, an analysis focused specifically on podocarp leaf traits would be advantageous. However, podocarps are not well represented in the global data set. The few data that are available suggest that leaf mass per area, leaf life spans, and photosynthetic capacity of podocarps are unremarkable, falling toward the middle of the range of values encompassed by conifers as a whole (Figures 9.2 and 9.3).

CANOPY RESIDENCE TIME AND COEXISTENCE OF ANGIOSPERMS AND CONIFERS

Bond's (1989) paper focused mainly on the likely impact of leaf and stem traits on relative performance of juvenile conifers and angiosperms, in an attempt to explain past and present habitat partitioning. One point not covered in his synthesis was the likely role of longevity differences in the coexistence of conifers and angiosperms in some forests. Chesson and Warner (1981) proposed that differences in adult longevity underlie persistence mixtures in many communities, including forests. The essence of this general hypothesis is that mixtures can persist if environmental fluctuation permits periodic recruitment of weak competitors that usually survive poorly as juveniles and if their adults are able to survive over long periods of poor recruitment. This "storage effect" is embodied by the dynamics of temperate conifer-angiosperm mixtures. Long canopy residence times enable conifers to coexist with angiosperms in many temperate forests, despite infrequent recruitment (Read and Hill, 1988; Lusk and Ogden, 1992; Carleton et al., 1996; Lusk and Smith, 1998). Data reviews have confirmed that conifers are appreciably longer-lived, on average, than angiosperm canopy trees in temperate forests of both Northern and Southern hemispheres (Loehle, 1988; Enright and Ogden, 1995). These poorly understood differences in longevity might ultimately prove at least as important as light environment partitioning (Lusk et al., 2009) in explaining the dynamics of tree species coexistence in these communities. Much less information on tree longevities is available from tropical forests, although radiocarbon dates suggest that some tropical *Agathis* species can attain ages of up to 1,000 years (Ogden, 1981). The role of longevity differences in explaining the dynamics of tropical forest communities is therefore unclear.

CONCLUSIONS

Developments during the last two decades shed light on several aspects of habitat partitioning between conifer and angiosperm trees. Bond's (1989) emphasis on vegetative traits and competitive ability of juveniles is largely vindicated by evidence of the constraints imposed by xylem and leaf traits on the performance of conifer seedlings. The present state of knowledge permits the generalization that conifers do best in habitats where fitness is more a function of nutrient conservation or cold resistance than of juvenile carbon gain potential and enables us to specify some of the mechanisms involved. More attention could be paid to the mechanisms underlying coexistence of conifer and angiosperm trees in some forests, despite the apparent competitive advantages of angiosperm juveniles. Likely mechanisms include differences in canopy residence time and impairment of angiosperm carbon gain by freeze-thaw embolism during cold weather.

APPENDIX: SOURCES OF CONDUIT DIAMETER DATA IN FIGURE 9.1

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A Functional Analysis of Podocarp Ecology

Timothy J. Brodribb

ABSTRACT. Viewed in terms of species diversity, the Southern Hemisphere conifer family Podocarpaceae is equivalent to its northern sister the Pinaceae. However, despite their similar age and common heritage these two families diverge strongly in morphology, physiology, and ecology. Both Pinaceae and Podocarpaceae are successful families of vascular plants, and in both cases this success has been built upon contrasting and rather canalized adaptive differentiation. Pinaceae thrive in virtually all Northern Hemisphere forest environments where freezing limits the success of evergreen angiosperm competitors. In contrast, the Podocarpaceae are most successful in the tropics, where they compete directly with broad-leaved angiosperms, usually in montane rainforest. This chapter discusses some of the key adaptations that have enabled tropical Podocarpaceae to remain competitive during the rise of angiosperms. I also examine the hydraulic “Achilles heel” that limits all members of the Podocarpaceae to a mesic rainfall envelope.

ADAPTATION TO LIFE IN TROPICAL FORESTS

Large, bilaterally flattened leaves are more efficient at harvesting light than spirally arranged needle or scale leaves (Leverenz, 1995; Pickup et al., 2005). This general rule is highly significant when considering the outcome of conifer–angiosperm competition in the period since angiosperm diversification in the Late Cretaceous. With the exception of *Gnetum*, gymnosperms appear to be incapable of producing large laminate leaves, and as such, they cannot benefit from the economic advantages of efficient light harvesting and minimal self-shading that broad leaves offer (Falster and Westoby, 2003). The overwhelming dominance of broad-leaved taxa in most productive regions of the tropics indicates that the benefits of large leaf size reach their peak in this region (Webb, 1968). Warm temperatures and an absence of stresses that could potentially limit leaf size, including cold, soil water deficiency, and abiotic mechanical damage in tropical rainforests, contribute to the predominance of large, flattened leaves. Given the adaptive bias toward large leaves in the tropics and the limited

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capacity in conifers to produce large leaves (Bond, 1989), the modern tropics appear hostile to most conifer families. Remarkably, the Podocarpaceae have evolved multiple anatomies that allow many species to elaborate flattened shoots or broad leaves which appear to be instrumental to the unusual success of the family in the tropics.

MORPHOLOGICAL FLATTENING IN SHORT SHOOTS

The most obvious adaptation in podocarps to affect large, flattened photosynthetic surfaces is the compression of short shoots to form two-dimensional photosynthetic

structures. Some 135 species of extant podocarps from 11 genera exhibit flattened or composite photosynthetic structures (Figure 10.1). Flattening of short shoots is achieved by twisting leaves at the base such that they are oriented parallel to the shoot axis and arranged in a manner typical of the leaflets on angiosperm compound leaves. Flattened shoots are displayed perpendicular to the stem axis, thereby maximizing light collection. Many independent origins of shoot flattening are known (Biffin et al., this volume), leading to an impressive diversity of shoot morphologies in the family. Multiveined "broad leaves" are also found in two genera of Podocarpaceae (*Nageia*

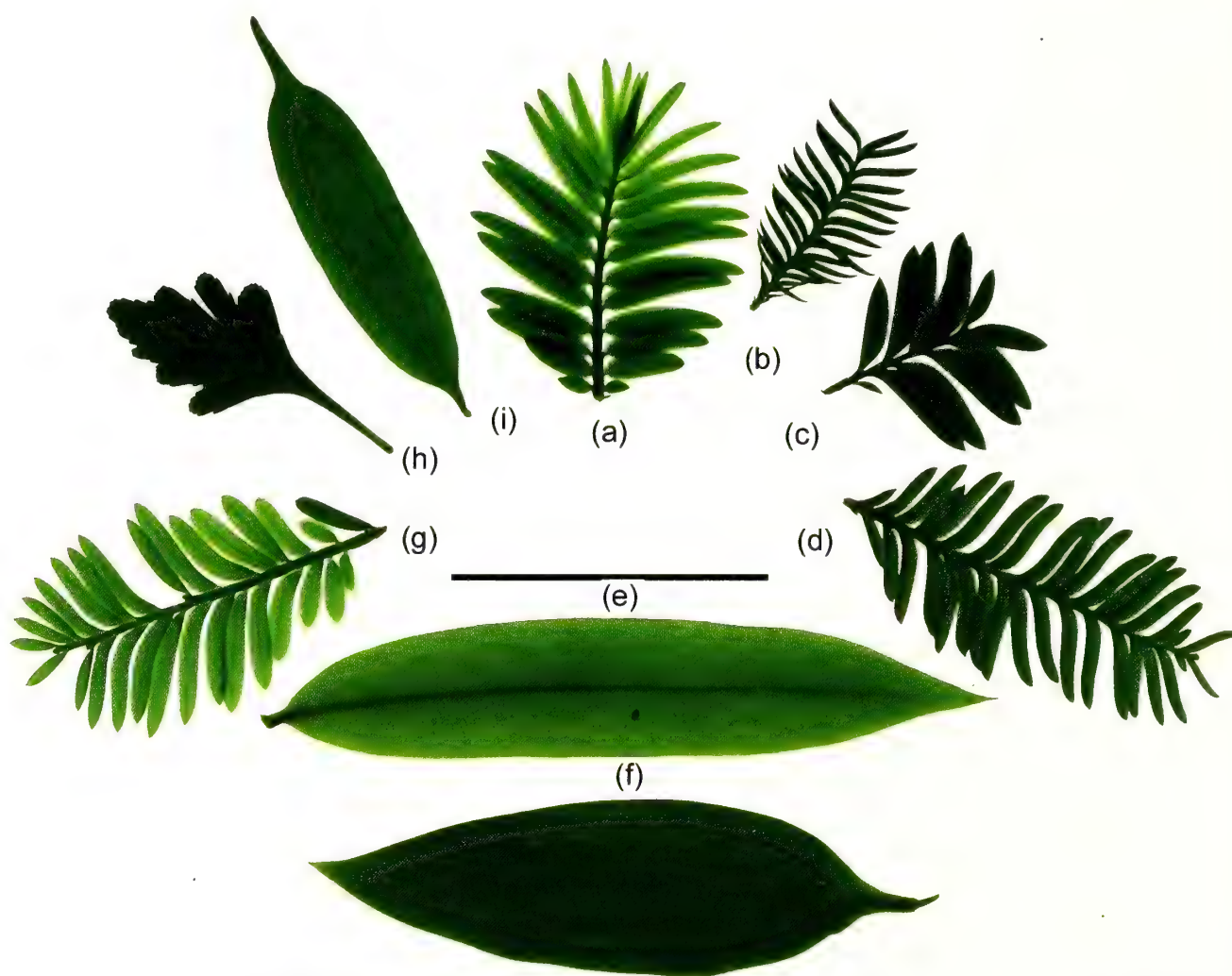


FIGURE 10.1. Some examples of the diversity of shoot flattening in nine genera of Podocarpaceae: (a) *Retrophyllum*, (b) *Dacrycarpus*, (c) *Falcatifolium*, (d) *Acropyle*, (e) *Podocarpus*, (f) *Nageia*, (g) *Prumnopitys*, (h) *Phyllocladus*, and (i) *Sundacarpus*. Along with obvious planation of short shoots (a, b, c, d, g), podocarps have evolved multiveined leaves (f) and phylloclades (h) and internal conducting sclereids (see text). Scale bar is 10 cm.

and *Phyllocladus*), the only genera outside the Araucariaceae with this capability. In *Phyllocladus* whole shoots are flattened into one multiveined lamina, and in the tropical species *P. hypophyllus*, flattened phylloclades are arranged into large structures that resemble the compound leaves of some palms.

The arrangement of leaves in two ranks flattened into a plane is not unique to podocarps, with some Northern Hemisphere conifer taxa such as *Sequoia*, *Metasequoia*, and *Taxodium* also exhibiting bilaterally compressed shoots. However, the Northern Hemisphere is overwhelmingly dominated by needle- and imbricate-leaved conifers, which constitute 96% of its total number of extant conifer species (Welch and Haddow, 1993). Shoots with strong bilateral compression are found only in six species in the Northern Hemisphere, all from the former Taxodiaceae. In marked contrast, about 60% of podocarp species produce distinct bilaterally flattened foliage (Hill and Brodribb, 1999).

ANATOMICAL ADAPTATION IN LEAVES

Most conifer species possess scale or needle leaves, and the absence of large-leaved conifer species can be traced to an apparent inability among extant conifers to form a reticulate plumbing network in the leaf lamina (Bond, 1989). The hydraulic efficiency conferred by vein reticulation is a prerequisite for elaborating large leaves because without an efficient means of distributing water evenly across the lamina, water deficits created by evaporation from the leaf during photosynthesis would lead to cell damage. The evolution of the hydraulic vascular system in plants saw nonliving pipes (xylem) create a “superhighway” for water flow through roots, stems, and leaves, avoiding cell-to-cell transport limitation. However, these pipes terminate within the leaves, at which point water must flow into the living mesophyll tissue, where it encounters a very high resistance to flow as it moves into and between cells. Maximum hydraulic conductance would be achieved if veins of xylem branched such that they contacted all living cells in the leaf, but no plant makes this enormously complex architectural investment. Instead, theory suggests that productive leaves must be internally structured such that evaporating cells are in close proximity to the vein terminals (Brodribb et al., 2007). Through the 400 million years of leaf evolution there have been many experiments with the vascular anatomy and architecture of leaves (Kenrick and Crane, 1991; Boyce and Knoll, 2002), but only two highly convergent patterns emerge as being linked with high productivity: dense

reticulate venation or needle leaves (Brodribb et al., 2007). In conifers, which typically possess a single vein in the leaf, narrowing of the distance from the vein to the leaf margin enables high hydraulic efficiency and photosynthetic rates in needle leaves.

Many members of the Podocarpaceae exhibit a different solution to transporting water through single-veined leaves, allowing them to partially overcome the narrow-leaf-width limitation that applies to most other conifers. In eight genera of Podocarpaceae, hollow sclereids extend radially from the midvein out toward the leaf margins (Figure 10.2). Cumbersomely labeled accessory transfusion tissue (ATT) (Griffith, 1957), these sclereids have been shown to be nonliving water-filled cells analogous to xylem cells, even in their pitted end wall connections (Figure 10.2). In genera such as *Podocarpus* and *Sundacarpus*, accessory transfusion tissue reaches its maximum development, forming a layer of water-conducting cells between the palisade and spongy mesophyll that connect to the midvein through the transfusion tissue. *Podocarpus* species with well-developed ATT are able to attain widths in excess of 30 mm (e.g., *P. dispersis*). In Podocarpaceae genera such as *Acmopyle*, *Falcatifolium*, and *Sundacarpus* the combination of accessory transfusion tissue and shoot flattening enables species to produce strongly planated shoots that attain a size and shape that falls within the range of associated rainforest angiosperm leaves.

SHOOT FLATTENING AND SHADE

In consideration of the economic advantages of broad leaves it appears likely that shoot flattening in Podocarpaceae is an adaptation that allows species to grow efficiently at low light (Brodribb and Hill, 1997), which may give podocarps the ability to compete with broad-leaved angiosperms in tropical forests. Strong support for this hypothesis was provided by a study of diverse conifer shoot morphologies in the Southern Hemisphere, which revealed that shoot flattening was associated with the light saturation characteristics of leaves (Brodribb and Hill, 1997). Photosynthesis in species with highly flattened leaves became light saturated at low light intensities relative to nonflattened shoots, resulting in an inverse correlation between shoot width and saturating light intensity. The low light requirement of rainforest podocarp leaves combined with the efficient light foraging that comes from shoot planation (Leverenz et al., 2000) makes podocarp foliage highly competitive in rainforest understory.

The unrivalled (among conifers) success of Podocarpaceae in competition with angiosperms in the tropics

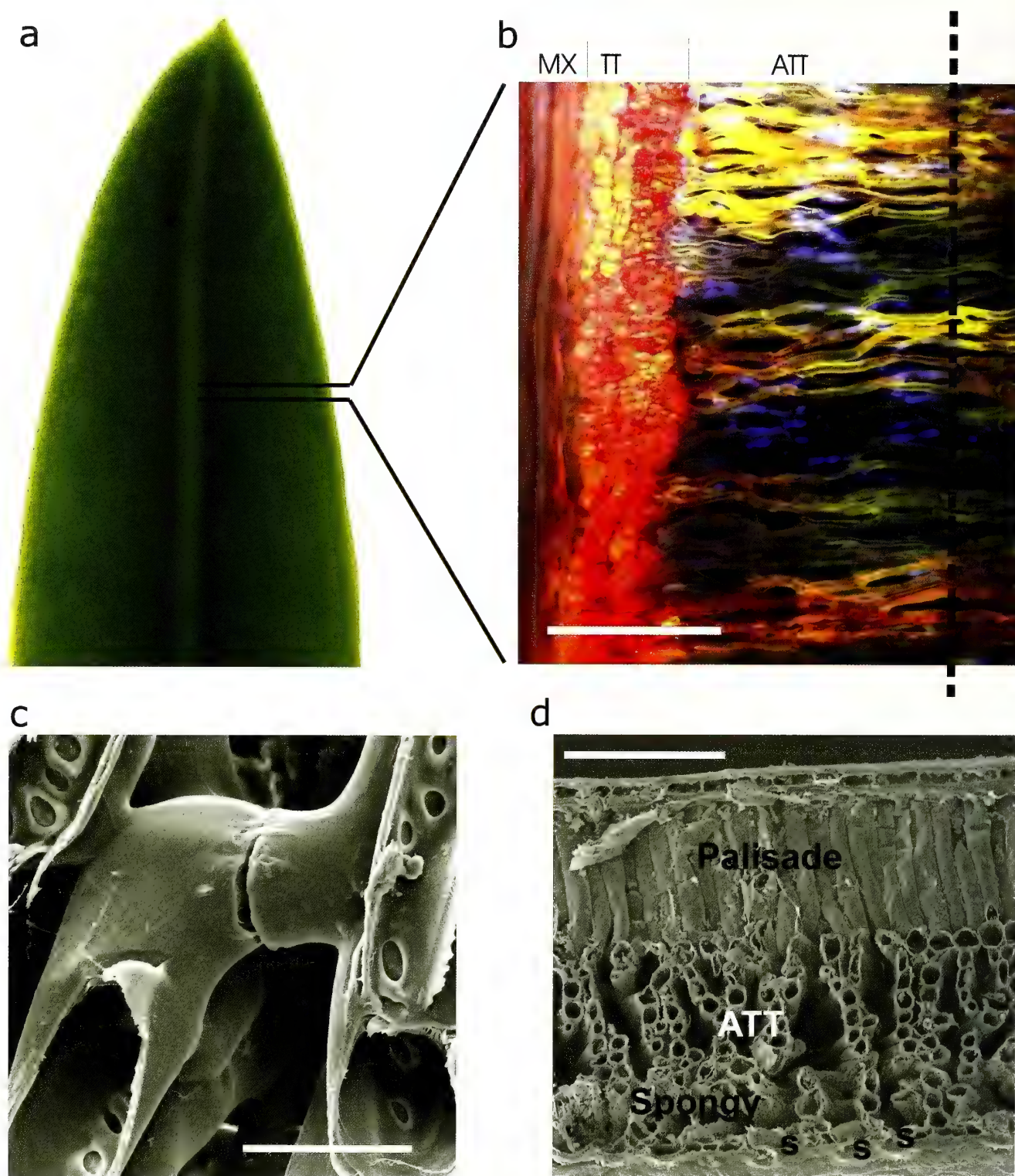


FIGURE 10.2. Anatomical features of the accessory transfusion tissue (ATT) that conducts water radially from the vein (a) toward the margin. Shown in paradermal section (b), these sclereids/tracheids form tubes conducting water away from the midvein (MX). Highly connected ATT cells (c) form a layer between the palisade and spongy mesophyll tissue (d). Scale bars are 200 μm (b, d) and 20 μm (c), and stomata are indicated by "s."

appears to be strongly linked to anatomical and morphological adaptations in the leaf that confer efficient growth in the shade. However, it should be noted that podocarp foliar architecture appears to be bound by functional limits that do not apply to the reticulate-veined broad leaves of angiosperms. It seems probable that ATT is a less efficient means of conducting water than reticulate venation, which may explain why maximum leaf size in podocarps never reaches the extremes seen in angiosperms. This is perhaps also why podocarps do not tend to be abundant in highly productive lowland tropical forests, in which angiosperm leaf size is at its maximum (van Royen, 1979). However, in montane forests, the flattened shoots of tropical Podocarpaceae are well inside the range of leaf sizes found in coexisting angiosperms (de Laubenfels, 1969). Considering the similar vegetative performance of podocarp and angiosperm leaves, it is not surprising that the diversity and success of podocarp species in tropical forests falls within the range of a number of moderately successful angiosperm families.

Podocarpaceae with flattened leaves or shoots first became successful in the early Cenozoic, demonstrating that these species were growing in forests with relatively dark understories (Hill and Brodribb, 1999; Brodribb and Hill, 2003). One possible explanation for the evolution of flattened shoots in podocarp foliage is that angiosperm evolution changed light quality in the conifer regeneration niche. The effect of this would have been either to force conifers into marginal habitats where canopy closure is delayed or incomplete or to favor the convergent evolution of broad leaves, as observed in podocarps.

LEAF ADAPTATION, SHADE TOLERANCE, AND TRANSEQUATORIAL MIGRATION

Podocarps have been successful in crossing the equator from their Southern Hemisphere origin to colonize the low latitudes of the Northern Hemisphere (see Morley, this volume). In contrast, only one species of Pinaceae has colonized south of the equator (*Pinus merkusii* at 2°S, Sumatra). Furthermore, Pinaceae have no fossil record in the Southern Hemisphere (Millar, 1998). An interesting alternative to vicariance as an explanation for the contrasting fortunes of *Pinus* in the Northern and Southern hemispheres is that evergreen tropical forests pose an impenetrable ecological barrier to the southward movement of *Pinus*. In contrast to podocarps, *Pinus* (and Pinaceae in general) have been relatively unadventurous in exploring flattened leaf morphologies, with the probable consequence that virtually all species are shade intolerant and

unable to regenerate beneath a forest canopy (for a review, see Richardson and Rundel, 1998). This conservative leaf morphology may underlie the inability of *Pinus* to penetrate the equatorial zone and into what appears suitable habitat (Grotkopp et al., 2002) in the Southern Hemisphere.

Pinus krempfii is an exception to the rule of Pinaceae exclusion from tropical rainforest. This extraordinary species comes to within a few degrees of the equator and uses specialized flattened leaves that confer the ability to regenerate in the shady forest understory. The leaves of *Pinus krempfii* show striking convergence with the flattened leaves of rainforest Podocarpaceae. Arrays of elongated sclereids in the mesophyll tissue of *Pinus krempfii* are highly reminiscent of those found in most broad-leaved podocarp species (Figure 10.3). According to leaf hydraulic measurements, these sclereids appear to be critical for facilitating radial water transport from the vein toward the leaf margin in broad, single-veined leaves in the same way as Podocarpaceae (Brodribb et al., 2007).

PODOCARPS AND DROUGHT

Considering their impressive ability to compete with angiosperms in the tropics, it is surprising the Podocarpaceae have only enjoyed limited success in temperate latitudes compared with the Pinaceae and Cupressaceae. I argue that the most significant agent preventing podocarp success at the higher latitudes of the Southern Hemisphere today is drought. A major drying trend in the temperate regions of the Southern Hemisphere through the late Tertiary coincides with a period of significant podocarp contraction and extinction in Australia and other southern landmasses (Kershaw et al., 1994). Diminishing rainfall, particularly during glacial periods, has resulted in a situation today whereby the podocarps from midlatitudes are confined to rainforest or wet montane forest and are absent from the dry woodlands that compose a large proportion of the forest cover in temperate Australia, Africa, and South America. The historical explanation for podocarp drought sensitivity most probably lies in the fact that the origins and diversification of the family are associated with cool and wet conditions on the continental margins of Gondwana (Hill and Brodribb, 1999). However the functional explanation seems to be linked to a disproportionately large trade-off in podocarp wood between construction cost and the ability to resist water stress.

Water tension increases in the xylem during soil drying and under extreme stress can become large enough

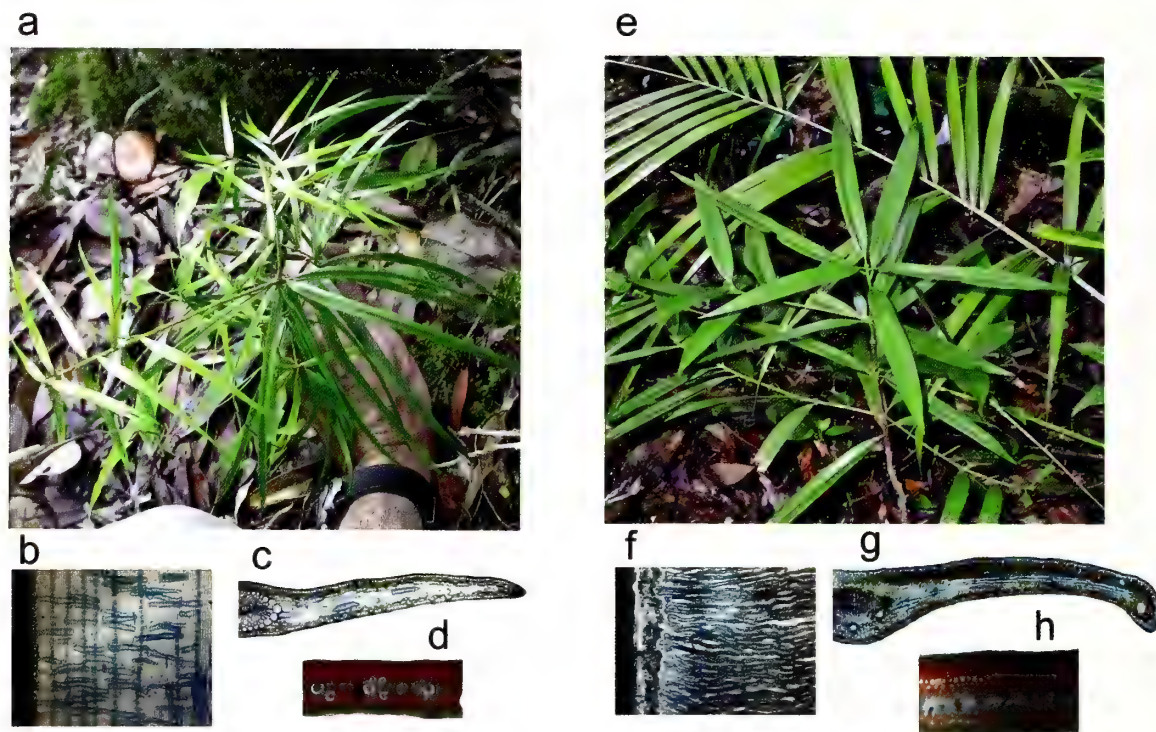


FIGURE 10.3. (a–d) *Pinus krempfii* and (e–h) *Podocarpus neriifolius* growing in the same tropical understory in Vietnam. Along with producing a similar flattened morphology, the *Pinus* leaves exhibit convergent anatomy that sees sclereids (blue) pass radially from the vein to the margin. Light microscope fluorescence images are paradermal (b, f), cross section (c, g), and tangential (d, h).

that air is drawn into the xylem conduits, cavitating the water in the lumen and causing them to cease functioning for water transport (Sperry and Tyree, 1990). The vulnerability of the xylem water column to water-stress-induced cavitation is an important measure of a plant's ability to survive drought (Tyree et al., 2002; Brodribb and Cochard, 2009). In Southern Hemisphere conifers, xylem vulnerability is closely linked to distribution according to the rainfall in the driest quarter (Brodribb and Hill, 1999). Podocarps sampled in this study occupied the wet end of the distribution-vulnerability scale (Figure 10.4). Consequently, drought sensitivity in podocarps has been associated with large extinction and range contractions in Australia since the establishment of the circumpolar current and the onset of glacial drying cycles (Brodribb and Hill, 2003).

Podocarp wood is not especially sensitive to dysfunction under water stress. Surprisingly, the range of hydraulic tensions associated with a 50% loss of xylem function is similar to that of Pinaceae, which appear to be far more tolerant of water stress. The unusual thing about podocarp

wood is its very high density relative to vulnerability. As with most plant groups, there is a clear trade-off in members of the Podocarpaceae between wood density and xylem vulnerability, with cavitation-resistant wood being considerably denser than drought-sensitive wood (Hacke et al., 2001). Strangely, the cost of producing cavitation-resistant wood is much greater in the Podocarpaceae than in either the Pinaceae or Cupressaceae; wood density of podocarp species is about 30% higher than Pinaceae and Cupressaceae species of equivalent cavitation resistance, whereas hydraulic efficiency is substantially lower in the podocarps (Pitterman et al., 2006). Therefore, it is probable that the high cost of drought resistance in podocarp wood is one of the reasons behind the weak competitiveness of podocarps in dry forest.

A second factor likely to limit podocarp success in drier forest is the very same tissue that makes the family so successful in the tropics. The leaf sclereids that allow podocarps to produce broad leaves (see above) are highly susceptible to collapse under water tension because of their unsupported arrangement in the mesophyll (Figure

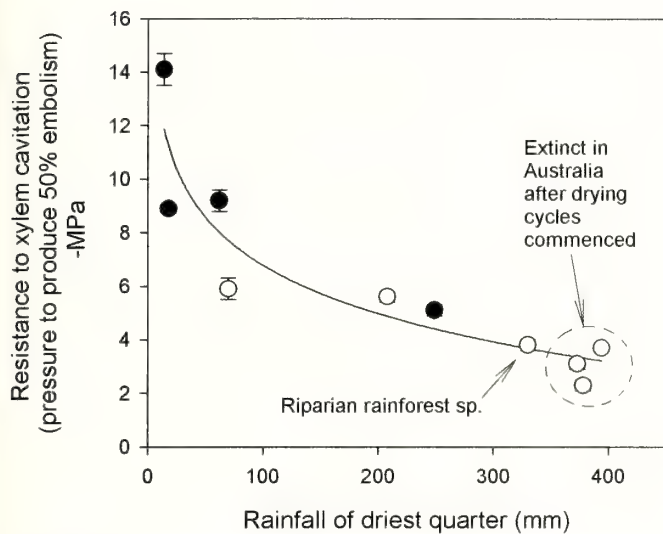


FIGURE 10.4. The relationship between xylem vulnerability to water-stress-induced cavitation and the driest natural range of Southern Hemisphere podocarps (open circles) and Cupressaceae (solid circles). Podocarps are the most vulnerable of the group, and genera at the wet end of the spectrum (within dashed circle) became extinct in Australia during Cenozoic drying. Another species appears to be at its rainfall limit in Australia, growing only on river edges in the wettest parts of Tasmania (*Lagarostrobos franklinii*, indicated by an arrow). Error bars represent standard deviations.

10.5). Despite their thick walls, leaf sclereids were found to collapse at moderate water tensions, causing a loss of hydraulic and photosynthetic function in the leaf (Brodrribb and Holbrook, 2005). One of the most drought-resistant podocarps, *Podocarpus drouynianus*, has very short foliar sclereids and leaves that are almost needles in width, supporting the idea that broad leaves and sclereids tend to limit the drought performance of the family. Shade

and drought tolerance are often considered as antagonistic directions for adaptation, and Podocarpaceae appear to follow such a pattern (Brodrribb and Hill, 2000). Such strong physiological canalization seems to be a characteristic of conifers.

In contrast to podocarps, many Pinaceae are extremely drought resistant, producing tough needle leaves with high photosynthetic rates (Lusk et al., 2003; Brodrribb and Feild, 2008). Once again, however, evolutionary canalization has proved highly limiting because the needle leaves of most Pinaceae are extremely inefficient in the shade, making them uncompetitive in tropical evergreen forests (Richardson and Rundel, 1998).

PINACEAE VERSUS PODOCARPACEAE

Pinaceae-dominated forest covers a significant proportion of the Northern Hemisphere, whereas podocarps constitute a tiny proportion of the Southern Hemisphere forest cover. The high degree of success of Pinaceae relative to Podocarpaceae in temperate latitudes can be largely attributed to the harsh continental climates prevalent in major northern landmasses, which produce strong seasonality and regular freezing that benefit Pinaceae. Freezing is the “great leveler” between conifers and angiosperms because it greatly narrows the hydraulic advantage of angiosperm wood (Feild et al., 2002). When ice forms in the xylem of trees, the probability that air bubbles will form and occlude the xylem upon thawing is related to the size of xylem conduits (Sperry and Sullivan, 1992). The tiny conduits that make up conifer wood are relatively impervious to freeze-thaw embolism, whereas the larger vessels of angiosperms are prone to embolism. In much of the Northern Hemisphere where Pinaceae dominate, major freezing events are common during winter months, resulting in the freeze-induced shutdown of angiosperms at temperate latitudes for much of the year. Northern

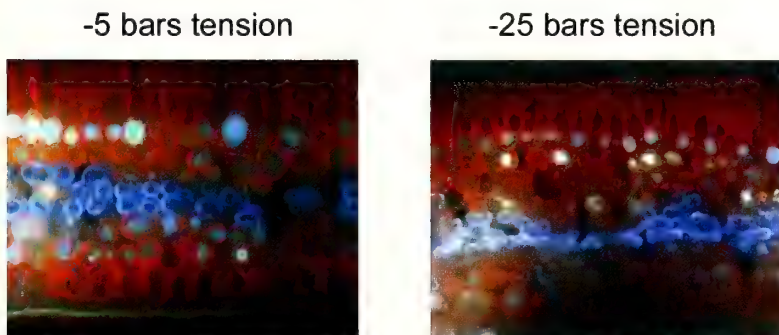


FIGURE 10.5. Tangential sections (cut parallel with the midrib) of a *Podocarpus grayei* leaf, showing accessory transfusion tissue cells (blue due to lignin fluorescence) in hydrated (–5 bars) and mildly water-stressed (–25 bars) leaves. Collapse of the accessory transfusion tissue under moderate water tension may limit podocarp success in drier climates.

Hemisphere conifers benefit greatly from the sensitivity of angiosperms to freezing, and this benefit can be clearly seen in terms of an increasing dominance of conifers moving poleward from the Tropic of Cancer. In contrast, the moderate seasonality experienced in most parts of the Southern Hemisphere means that podocarps do not benefit from the freeze-thaw advantage of its Pinaceae sister except at high latitudes and altitudes. As such, podocarps have a greatly diminished opportunity for the type of biome domination achieved by Pinaceae at higher latitudes in the Northern Hemisphere.

One question that remains is why Podocarpaceae are absent from most of the Northern Hemisphere. Biogeography probably plays a role in driving this pattern, given the relatively recent north-south contacts through Southeast Asia and Central America (Morley, this volume; Dalling et al., this volume). However, considering the demonstrated potential of podocarps for long-distance dispersal (fleshy cones and conspicuous presence on many recent disjunct islands such as Samoa, Fiji, and Cuba), biogeography alone is insufficient to explain the apparent inability of podocarps to colonize seasonal northern habitats. Plant functional limitations also provide a possible insight into the exclusion of podocarps from the Northern Hemisphere. Because of a comparatively warm evolutionary history podocarps appear to have relinquished some of the characteristics that confer freeze tolerance. The water transport characteristics of both wood and leaves of podocarps appear to be poorly adapted to regular sap freezing. Ice formation has a tendency to desiccate the vascular tissue in a similar fashion to drought. Ice has a very low water potential and is able to draw water out of xylem tissue, mimicking the effect of dry soil. As discussed above, podocarps are ill adapted to respond to desiccation stress, and this may contribute to an inefficient response to the types of freezing stresses that regularly occur in the Northern Hemisphere. The other freezing handicap for podocarps is the presence of leaf sclereids, which are likely to form a nucleation center for ice formation in the leaf. In contrast, the Pinaceae appear to have been largely canalized in the opposite direction by diversification in freezing climates, which has culminated in the pines that produce some of the most freeze-tolerant foliage found in any plant group. As such, podocarps are unlikely to be successful in competition with Pinaceae in freezing environments in the Northern Hemisphere. Further work is required to formally quantify the impact of these freezing liabilities for podocarps, but the fact that the podocarps are poorly represented in all but the wettest Southern Hemisphere tree lines suggests that they may not be well suited to the

extended seasonal freezing that characterizes much of the Northern Hemisphere.

CONCLUSIONS

The podocarp capacity to successfully compete with angiosperms in tropical forests is unusual among conifers. The success of the Podocarpaceae can be traced to anatomical and morphological modification of leaves and shoots to produce large foliar units that function similarly to broad leaves in angiosperms. Large foliar units in podocarps probably originated in the Late Cretaceous and may have been a response to angiosperm radiation (Biffin et al., this volume). The economic advantages conferred by the broad leaves and shoots of podocarps are significant in productive tropical forests, but associated limitations appear to prevent podocarps from achieving the degree of success in either the northern or southern temperate latitudes enjoyed by Pinaceae in the Northern Hemisphere.

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Podocarp Roots, Mycorrhizas, and Nodules

Ian A. Dickie and Robert J. Holdaway

ABSTRACT. Podocarps are often found on low-nutrient soils and further exacerbate nutrient limitation through the production of recalcitrant litter. Understanding podocarp ecology therefore depends on understanding the root adaptations of podocarps to obtain nutrients. The roots of podocarps are heterorhizic (having two root forms) with abundant spherical determinate short roots, a unique form of largely unknown function, as well as indeterminate fine roots. There is no strong evidence for nitrogen fixation in the nodules. Although nodules are frequently and abundantly colonized by arbuscular mycorrhizal fungi, they are neither required for mycorrhizal infection nor dependent on mycorrhizal infection for their development. The fungal symbiont community associated with podocarps does not appear to be distinctive from that of other plants at a global scale, although it may differ from co-occurring plants within a site. Perhaps the most obvious, yet largely overlooked, hypothesis is that the form of the nodules is the function. The presence of nodules permits a doubling of root cortex volume, while simple geometry indicates that a spherical form involves the lowest possible cost in producing cell wall and membrane material per unit of root volume. Increased root volume permits greater arbuscular mycorrhizal interaction, and hence, nodules may be analogous to the determinate ectomycorrhizal roots of the Pinaceae as a structure to maximize fungal interactions at minimal root construction cost.

INTRODUCTION

Podocarps (gymnosperms in the Podocarpaceae) grow on a range of soils from relatively fertile (e.g., C:N and C:P ratios of 12.6 and 394; Solomon et al., 2002) to infertile soils with most mineral nutrients locked into organic forms (e.g., C:N ratios = ~40, C:P ratios > 1,000; Armesto et al., 1995; Coomes et al., 2005). Nonetheless, it is the ability of podocarps to grow and compete on infertile sites that explains their occurrence in lowland tropical habitats (e.g., Kitayama et al., this volume) and their dominance on older, relatively phosphorus-limited temperate sites (Richardson et al., 2004; Coomes et al., 2005; Coomes and Bellingham, this volume). On higher-phosphorus soils, podocarps are more likely

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to be outcompeted by ferns and angiosperms (Coomes et al., 2005; Carswell et al., 2007) and may show negative growth and survival responses to phosphorus or mixed-fertilizer addition (Carswell et al., 2003; Pareliussen et al., 2006). Where present, podocarps can exacerbate mineral nutrient limitation through the production of relatively low quality, high-carbon leaf litter, which can lock mineral nutrients into unavailable forms (Wardle et al., 2008). This litter decomposes so slowly that it can remain obvious more than 40 years after the death of a podocarp tree (Wardle et al., 2008). Understanding podocarp ecology therefore requires an understanding of the mineral nutrient uptake strategies that allow the persistence of podocarps on low nutrient soils.

In this chapter we examine the root adaptations of podocarps that permit efficient mineral nutrient acquisition from low-nutrient soils, both in terms of maximizing nutrient uptake and minimizing costs. We focus on two key questions: (1) Are there unique aspects of the mycorrhizal associations of podocarps that permit them greater mineral nutrient access on low-nutrient soils? (2) What, if any, is the functional role of nodules in podocarp mineral nutrient uptake?

MYCORRHIZAL ASSOCIATIONS OF PODOCARPS

Podocarps are arbuscular mycorrhizal, forming symbiotic associations between plant roots and fungi in the Glomeromycota. In these symbioses the plant provides carbon to the fungus, and the fungus greatly increases plant acquisition of phosphorus (Smith and Read, 2008). The presence of arbuscular mycorrhizas is typical of more than 50% of gymnosperm species, with the remainder, comprising the Pinaceae and Gnetaceae, primarily forming ectomycorrhizas (Brundrett, 2009). This potentially reflects a close phylogenetic relationship between these two families (Hajibabaei et al., 2006; Wu et al., 2007), although Brundrett (2009) argues for separate evolution of ectomycorrhizas in these groups. Although there are sporadic reports of ectomycorrhiza in other gymnosperms (e.g., Cupressaceae, *Wollemia*), these appear to reflect misdiagnosis or atypical definitions of ectomycorrhizas (Brundrett, 2009). Arbuscular mycorrhizas are also typical of 74% of angiosperms, including many of the plant species frequently associated with podocarps (Brundrett, 2009).

Arbuscular mycorrhizal infection of podocarp roots is generally extremely dense. In New Zealand temperate podocarps, there are reported infection levels of

88%–96% of root length (Hurst et al., 2002); our own observations indicate that nearly 100% of available root length (fine roots capable of forming arbuscular mycorrhizas) is infected across a number of temperate podocarp species (I. A. Dickie, unpublished data). These levels of arbuscular mycorrhizal infection are higher than many other plants and significantly higher than some, but not all, co-occurring angiosperms.

Arbuscular mycorrhizas benefit plants by increasing the effectiveness (extent of soil exploration) and efficiency (benefit:cost ratio) of phosphorus uptake (Koide et al., 1999). Phosphorus is relatively immobile in soil, so the extensive hyphae of arbuscular mycorrhizal fungi provide a greatly increased ability to explore the soil volume. The relative dependence of plants on mycorrhizal infection is generally strongly correlated with plant root traits (Baylis, 1975; St John, 1980). Species with high specific root length (length/mass) and abundant and long root hairs are expected to have relatively lower dependence on mycorrhizal fungi than species with thick, higher-cost roots and fewer root hairs.

There have been few studies of podocarp root morphology, but our own observations suggest a moderately coarse root system (mean diameters ~0.60 mm; specific root length $711 \pm 85 \text{ cm g}^{-1}$, mean \pm standard error), with abundant root hairs in some species (Figure 11.1). Observed root diameters are consistent with the concept of podocarps having a high mycorrhizal dependency (St John, 1980); however, the production of abundant root hairs in some podocarps is not. The presence of abundant and long root hairs and mycorrhizas may indicate they have different functions in mineral nutrient uptake or that they have complementary functions under conditions of poor mineral availability.

IDENTITY OF THE FUNGAL SYMBIONTS OF PODOCARPS

Like all arbuscular-mycorrhizal symbiosis, the fungi that form arbuscular mycorrhizas with podocarps are in the Glomeromycota (Schüssler et al., 2001). The fungi appear typical of arbuscular mycorrhizal communities in general, with a dominance of *Glomus* species and less common *Archaeospora* and *Diversisporaceae* (Russell et al., 2002; Wubet et al., 2006). Two studies might be taken to suggest a degree of host specificity to podocarps. Wubet et al. (2006) found distinct fungal species associated with co-occurring *Juniperus procera* (Cupressaceae) and *Afrocarpus falcatus* (Podocarpaceae). Further, in a study of four species of podocarps, Russell et al. (2002) found little similarity between sequences of Glomeromycota

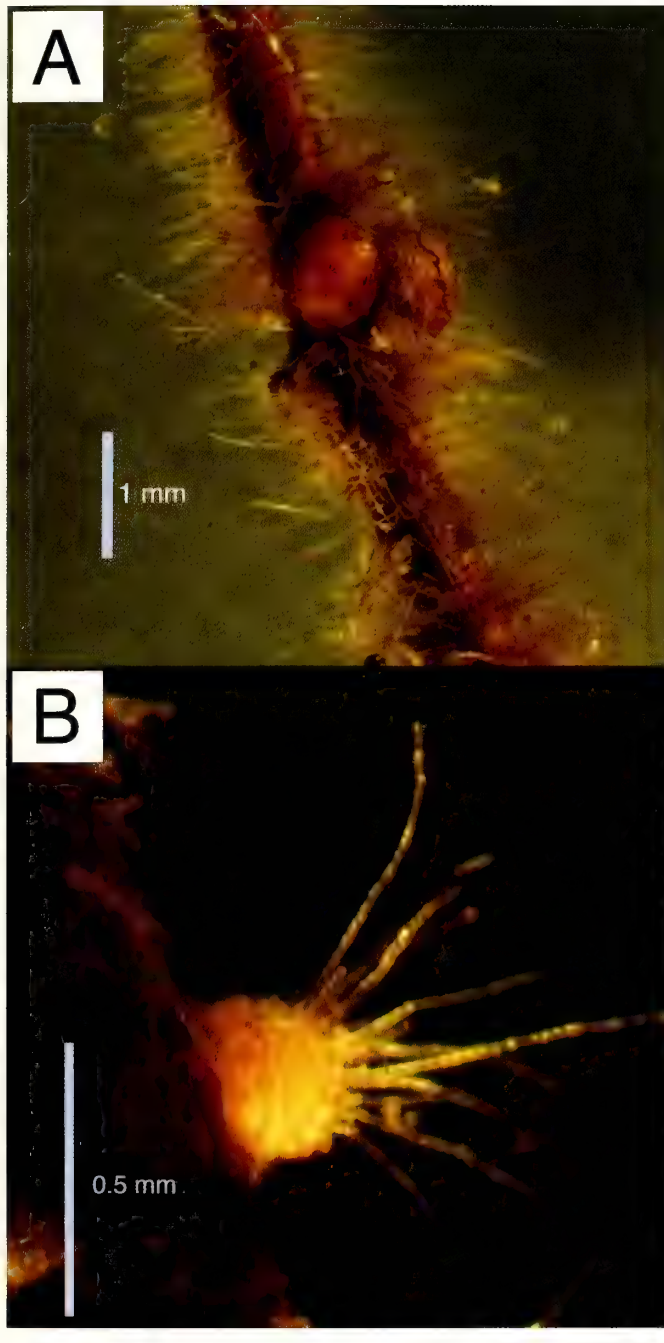


FIGURE 11.1. Abundant root hairs on podocarps occur both (A) on long roots, as seen on *Prumnopitys ferruginea*, and (B) sometimes on nodules, as seen on *Phyllocladus alpinus*. Images by the authors.

from podocarp roots and existing sequences in GenBank (<http://www.ncbi.nlm.nih.gov>). Nonetheless, at least the results from Russell et al. (2002) may reflect the paucity of Southern Hemisphere Glomeromycota sequences (particularly in 2002), rather than true host specificity. Using

the ribosomal (18s, internal transcribed spacer [ITS]) sequence data from Russell and colleagues (GenBank Accession numbers AF452624–AF452636), we reexamined these sequences against GenBank to assess affinities with more recent collections (Table 11.1). Twelve of the 13 sequences matched at 95% or greater maximum identity to other sequences in GenBank, of which three matched only sequences from New Zealand, five had nearest matches to sequences from elsewhere in the Southern Hemisphere, and four had nearest matches to sequences from the Northern Hemisphere. There was no evidence of any specificity of these fungi to podocarps—the nearest matches included liverworts, grasses, and a range of angiosperms, with no matches to other podocarps. Therefore, the arbuscular mycorrhizal fungi colonizing podocarps may be distinct from other host plants within a site (Wubet et al., 2006), but on a broader scale the fungi associating with podocarps do not appear to be particularly distinctive. Apparent host specificity within sites may reflect the strong effects of individual podocarp trees on soil chemical and biotic properties (Wardle et al., 2008) influencing local fungal community composition.

ROOT NODULES OF PODOCARPS

The roots of the podocarps are characterized by abundant spherical protuberances, often referred to as “nodules” (Figure 11.2). Thus, podocarps are heterorhizic, having two distinct root forms: long indeterminate roots and determinate nodules. Initial nodule formation typically occurs as regularly spaced spheres developing in multiple rows along the length of fine roots, with substantial variation among plants in the regularity of nodule formation. Nodules arise from the root pericycle, similar to lateral root development (Russell et al., 2002), and are characterized by the absence of any apparent meristematic tissue or root cap (Khan and Valder, 1972). As nodules age, epidermal cell walls become thicker, and the color of the nodules becomes increasingly dark (Russell et al., 2002). Russell et al. (2002) noted that starch reserves were high in nodule cortical cells prior to arbuscular mycorrhizal colonization and were depleted in heavily colonized cells. In some cases, older nodules are shed and can become abundant in soil. After shedding old nodules, nodule formation may be reinitiated at the same location. In an interesting variation, it is also possible for apical growth to resume, potentially contributing to the formation of chains of nodules (discussed below). The unique form of podocarp nodules has led to a number of hypotheses about their functional

TABLE 11.1. Re-BLAST (basic local alignment search tool) searching of sequences from Russell et al. (2002) against GenBank, showing best match (if greater than 95% similarity) to arbuscular mycorrhizal associates of known host plants or plant communities. There is no evidence of host specificity to podocarps; N/A indicates not applicable.

Sequence from Russell et al. (2002)	Sequence name	Best match (>95%)	Identities	Host plant	Host plant taxonomic group	Collection location
AF452624	PODO17.1	EU417643.1	509/519 (98%)	<i>Sciaphila ledermannii</i>	Triuridaceae	Cameroon
AF452625	PODO17.2	AF452625.1	305/305 (100%)	<i>Juglans neotropica</i>	Juglandaceae	Ecuador
AF452626	PODO17.3	AJ716326.1	878/886 (99%)	<i>Marchantia foliacea</i>	Marchantiales	New Zealand
AF452627	PODO16.1	AJ699064.1	552/557 (99%)	<i>Marchantia foliacea</i>	Marchantiales	New Zealand
AF452628	PODO16.2	AJ699068.1	1,010/1,046 (96%)	<i>Marchantia foliacea</i>	Marchantiales	New Zealand
AF452629	PODO1.1	DQ336488	173/181 (95%)	<i>Guarea pterorhachis</i>	Meliaceae	Ecuador
AF452630	PODO1.2	EU152178	508/510 (99%)	<i>Tabebuia chrysantha</i>	Bignoniaceae	Ecuador
AF452631	PODO1.3	AM384971	373/384 (97%)	<i>Thymus pulegioides</i>	Lamiaceae	Switzerland
AF452632	PODO7.1	AM268195	549/564 (97%)	Grassland	Various	Finland
AF452633	PODO7.2	FJ483156	520/529 (98%)	Freshwater marsh	Various	United States
AF452634	PODO7.3	AM420382	566/580 (97%)	Aquatic macrophyte	Unclear	Norway
AF452635	PODO18.1	EU159171	499/499 (100%)	Neotropical rainforest	Various	Ecuador
AF452636	PODO18.2	None	Best match only 94%	N/A	N/A	N/A

significance. Despite nearly 100 years of research on this subject, a clear explanation has yet to emerge.

PLANT PHYLOGENY AND OCCURRENCE OF NODULES

Within the gymnosperms, nodulated roots are present in the Podocarpaceae, Phyllocladaceae, and Araucariaceae, which form a single phylogenetic group, and *Sciadopitys* (Khan and Valder, 1972), which Stevens (2001–2009) suggested is a distinct but closely related clade (Figure 11.3). Nodules in the Araucariaceae and *Sciadopitys* were reported as less regular and more elongated and variable in size than nodules in podocarps (Khan and Valder, 1972), but we have observed regular, spherical nodules in *Agathis australis* (Araucariaceae; personal observation). Nodules are absent from the Cupressaceae and Taxaceae.

Outside of the gymnosperms, mycorrhizal nodules have been reported in a number of angiosperms, including *Gymnostoma* (Casuarinaceae; Duhoux et al., 2001), *Aesculus* (Sapindaceae; Khan, 1972), and several Caesalpiniaceae (Béreau and Garbaye, 1994). It is not clear that these other nodules are physiologically or genetically related to podocarp nodules. Khan and Valder (1972) outlined two traits as defining true podocarp-type nodules:

(1) development as a normal feature of roots, not being dependent on any microorganism for their development (Baylis, 1969), and (2) being fully differentiated structures with no root cap or apical meristem and with an endodermis surrounding and overarching the vascular strand.

The second of these defining traits must be taken as temporally dynamic, as both the initial growth and, particularly, the reinitiation of apical growth in some nodules implies an apical meristem. Nonetheless, none of the nonpodocarp nodulated roots have been shown to fit these criteria. In *Gymnostoma*, nodules do not form as a normal feature of the root, as the presence of soil microorganisms is required to induce nodule formation. Additionally, nodules in *Gymnostoma* have an apical meristem, and no evidence of an endodermis overarching the vascular strand was reported (Duhoux et al., 2001). The nature of nodule formation in *Aesculus* remains unclear, because the one attempt to synthesize nodules in the absence of soil microbes failed to maintain soil sterility over the course of the experiment (Khan, 1972).

There are occasional reports of nodules in other groups; however, these appear to be based on confusion between beaded roots and true podocarp-type nodules (Khan and Valder, 1972). Beaded roots are a commonly

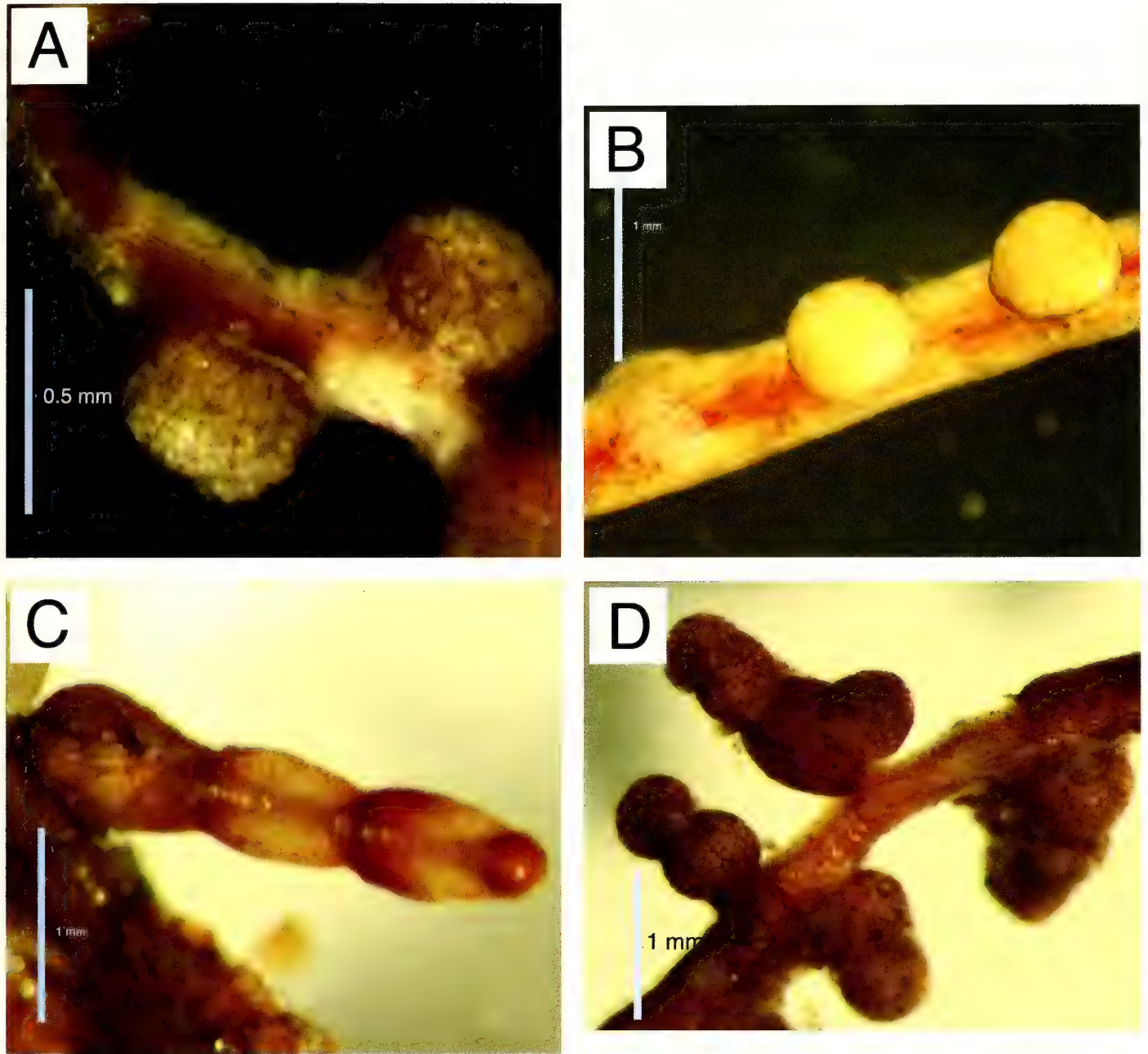


FIGURE 11.2. Examples of variation in form among nodules and roots: (A) very small nodules on *Lepidothamnus intermedius*, (B) formation of nodules (three stages of development) of regularly spaced uniform nodules in *Dacrydium cupressinum*, (C) beaded roots (not nodule) in *Dacrydium cupressinum* (note the stele passing through beads and to the end of root with no overarching cortical cells), and (D) chained or beaded nodules in *Manoao colensoi*. A range of species are shown, but significant variation can also be found within species. Images by the authors.

observed root form in many tree species, where roots are regularly segmented by narrow constricted regions. Although beaded roots have occasionally been reported as being either ectomycorrhizal (Mineo and Majumdar, 1996) or arbuscular mycorrhizal structures (Grand, 1969),

it appears that beaded roots are not directly related to mycorrhizas or other soil organisms (Kessler, 1966; Beslow et al., 1970; Thomson et al., 1990). The development of beaded roots may reflect episodic growth linked to fluctuating soil moisture (Kessler, 1966), although this result

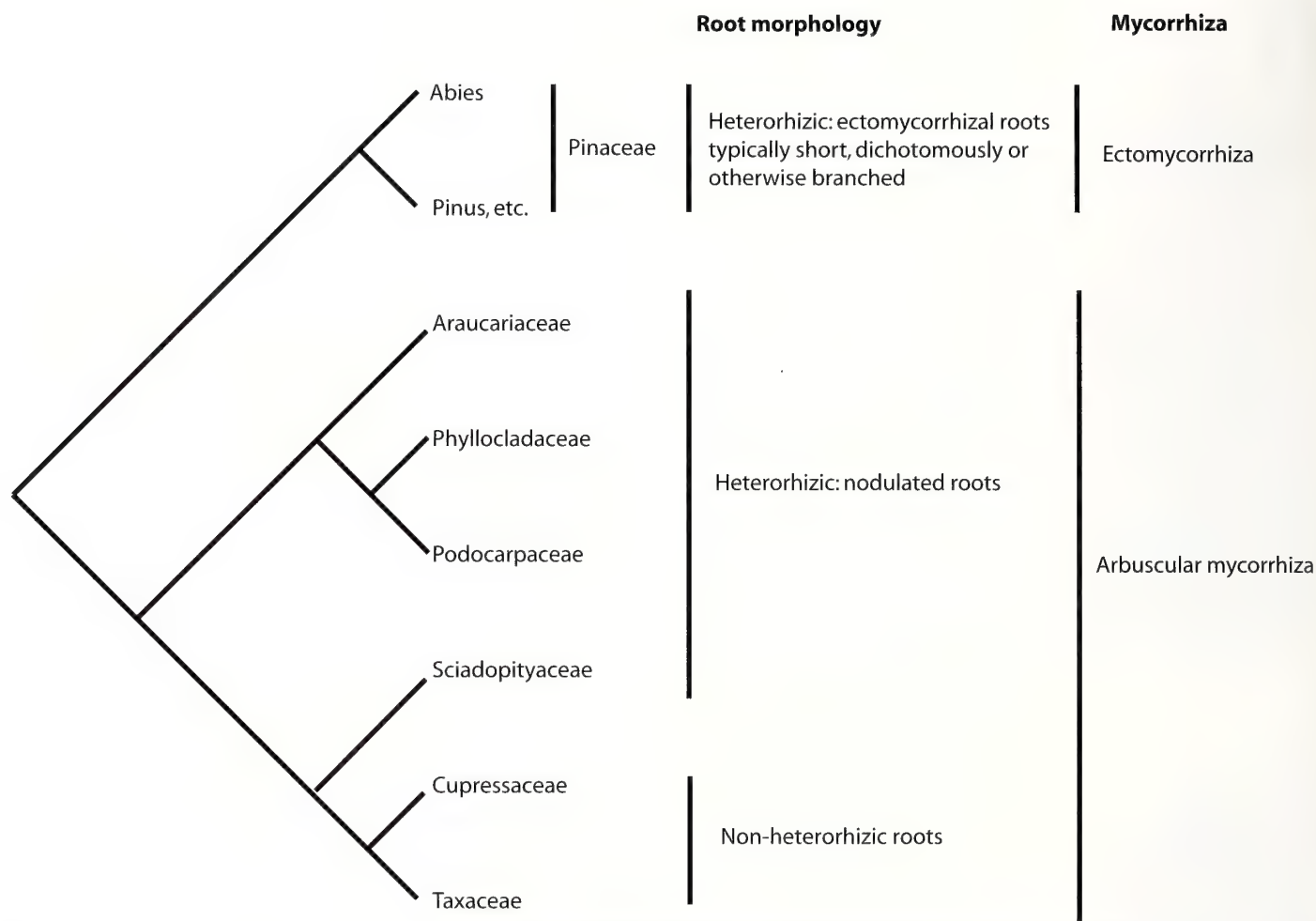


FIGURE 11.3. Phylogeny of the Pinales with mycorrhizal status and notes on root nodule morphology. Phylogeny follows Stevens (2008), who attempted to reflect current consensus. The podocarps share arbuscular mycorrhizas with the Cupressaceae and Taxaceae, but the presence of heterorhizic roots (i.e., short determinate roots distinct from long roots) shows similarity to the Pinaceae. Note that arbuscular mycorrhizas are also present in the Pinaceae, but ectomycorrhizas dominate (Horton et al., 1998).

is not consistent across studies (e.g., Beslow et al., 1970). Nonetheless, beaded roots retain meristematic tissue and have no overarching cortex and are, therefore, distinct from true podocarp-type nodules. Some podocarps form beaded roots in addition to nodules (Figure 11.2c), and some podocarp nodules develop apically on previously formed nodules, creating a beaded-nodule chain (Figure 11.2d). Perhaps it is not surprising that this has led to considerable confusion.

NITROGEN FIXATION AND PODOCARP NODULES

There have been a number of studies that claim to show low levels of nitrogen fixation in podocarp nodules

(e.g., Morrison and English, 1967; Grobbelaar et al., 1971) and others that fail to find any nitrogen fixation (Baylis, 1969). Morrison and English (1967) reported the presence of an endophyte resembling an actinomycete but give no further details. There was also a recent report of the isolation of *Rhizobium* (along with detection of weak nitrogenase activity) from *Podocarpus macrophyllus* roots with nodules (Huang et al., 2007). Nonetheless, on the whole, the evidence for nitrogen fixation in nodules is weak. The levels of nitrogen fixation reported in podocarp nodules are typically described as very low. Where low levels of nitrogen fixation have been reported, they may reflect nitrogen fixation by free-living rhizobium in soils or associated with roots, rather than a true symbiosis.

This was effectively demonstrated by Silvester and Bennett (1973), who showed that acetylene reduction (a proxy for nitrogen fixation) was uniformly associated with the soil or surface of roots and nodules of five species of nodulated gymnosperm, with no evidence of acetylene reduction in root nodules following a relatively mild surface sterilization.

The interest in nitrogen fixation in podocarp nodules appears to largely be driven by a superficial resemblance to rhizobial nodules, leading Khan and Valder (1972:40) to state "It is unfortunate that the word 'nodule' should have been applied at all...Had they been given a different name to begin with, it is doubtful whether confusion would ever have arisen in the literature concerning their function and mode of origin." Confusion between mycorrhizas and nitrogen fixation is by no means restricted to podocarps; some of the history and causes of this confusion are reviewed by Mikola (1986).

Although there is no good evidence of symbiotic nitrogen fixation in podocarp nodules, the potential importance of asymbiotic free-living or root-associated nitrogen fixation should be an area for further investigation. Asymbiotic nitrogen fixation can supply significant amounts of nitrogen in *Agathis australis* forests (Silvester, 2000) and in other forest systems (Reed et al., 2008) and may play a similar role in podocarp forests (Silvester and Bennett, 1973). Alternatively, a lack of available phosphorus under podocarps, partially driven by low litter quality, may limit the extent of asymbiotic fixation (Reed et al., 2008).

ARBUSCULAR MYCORRHIZAL INFECTION OF NODULES

The roots and nodules of podocarps are abundantly colonized by arbuscular mycorrhizal fungal hyphae (Figure 11.4). Nonetheless, Breuninger et al. (2000) note that the extensive arbuscular mycorrhizal structures in normal fine roots of *Araucaria* suggest that nodules may not play a major role in mycorrhizal associations. Our own observations support this, with extensive infection of long root cortical cells common in podocarps. Further, nodules do not require mycorrhizal fungi for their formation (Bailis, 1969). The presence of arbuscular mycorrhizal fungi is therefore neither a prerequisite for, nor dependent on, nodule formation.

There is some confusion around the question of whether extraradical mycorrhizal hyphae are associated with nodules. The extraradical hyphae are the portion of the arbuscular mycorrhizal fungal mycelium where active nutrient uptake from the soil solution occurs; hence, a lack of extraradical hyphae would imply an atypical, perhaps

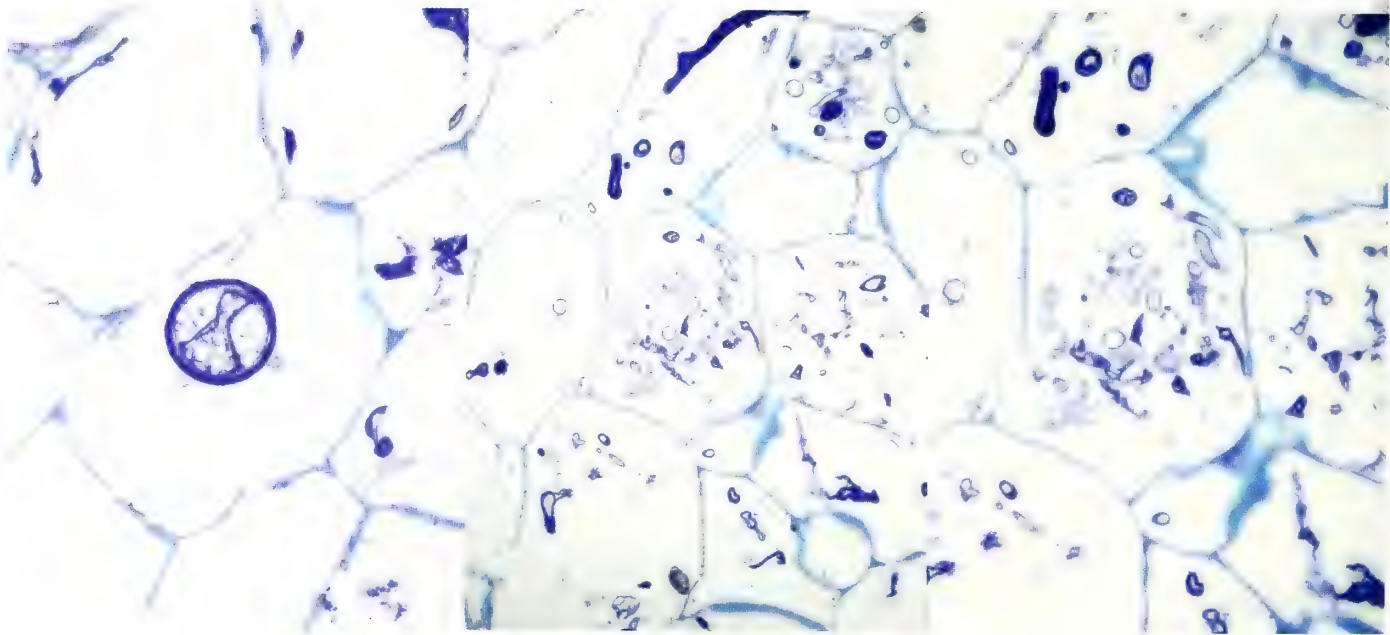
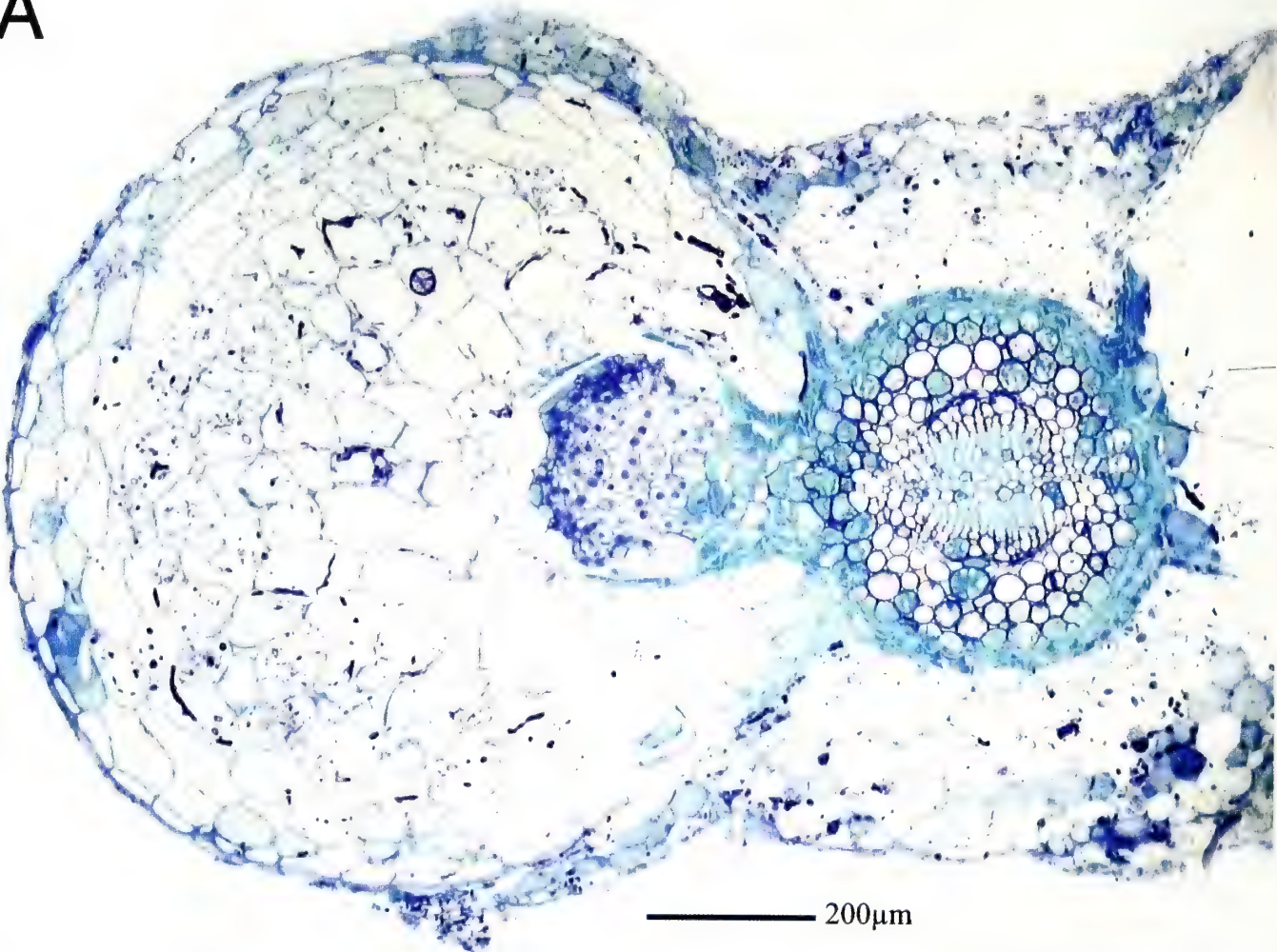
parasitic, mycorrhizal association. The outermost layers of podocarp nodules were reported as "mainly free of hyphae" by Russell et al. (2002), but McGee et al. (1999) showed sparse hyphae in epidermal cells. Epidermal cells in podocarp nodules have notable thickening of cell walls on mature nodules, which may lend support to the idea of limited fungal penetration through the epidermis. Nonetheless, the occurrence of dense fungal colonization in the cortex with only sparse colonization of outer layers is actually quite typical for all plant species: arbuscular mycorrhizal fungi penetrate a small number of epidermal cells, pass through the "exodermis" layer just below the epidermis (if present), and then proliferate in the cortex. Extensive arbuscular mycorrhizal hyphae on the surface of nodules of *Araucaria* were shown by Breuninger et al. (2000). In our own observations of *Podocarpus*, *Dacrydium*, and *Prumnopitys* we have observed frequent hyphae on the surface of nodules, what appear to be typical appresoria (cell penetration arises from appresoria), and hyphae that penetrate the surface of nodules. We therefore conclude that there is an extraradical mycelium with apparently typical attachment to the internal infection of root nodules by arbuscular mycorrhizal fungi and that prior reports of the absence of extraradical hyphae are incorrect.

Whether the arbuscular mycorrhizal fungi infecting nodules are distinct species from those infecting other roots on the same plant remains unknown. As observed by Russell et al. (2002), the determinate growth form of nodules places a constraint on fungal colony growth compared to long roots, as hyphal spread along a growing root is not possible. Russell et al. (2002) did observe, however, that fungal hyphae from the disintegrating cortex of old nodules were able to infect newly forming nodules.

REPLACEMENT OF NODULES

Root nodules, similar to fine roots in other species, have a limited life span (Eissenstat and Yanai, 1997). Nodules may be shed by the plant, with regrowth of new nodules at the same location. In other cases, nodules are formed in strings of connected nodules, which may reflect apical regrowth. The replacement of nodules is unlikely to be driven by declines in local soil fertility as there is little to be gained by replacement in the same location. Instead, there may be physiological changes in the nodules that render them increasingly inefficient with age. At least three hypothetical mechanisms may be involved. First, arbuscules, the site of nutrient transfer, are short-lived structures in most plants. In podocarps, collapsed fungal arbuscules

A



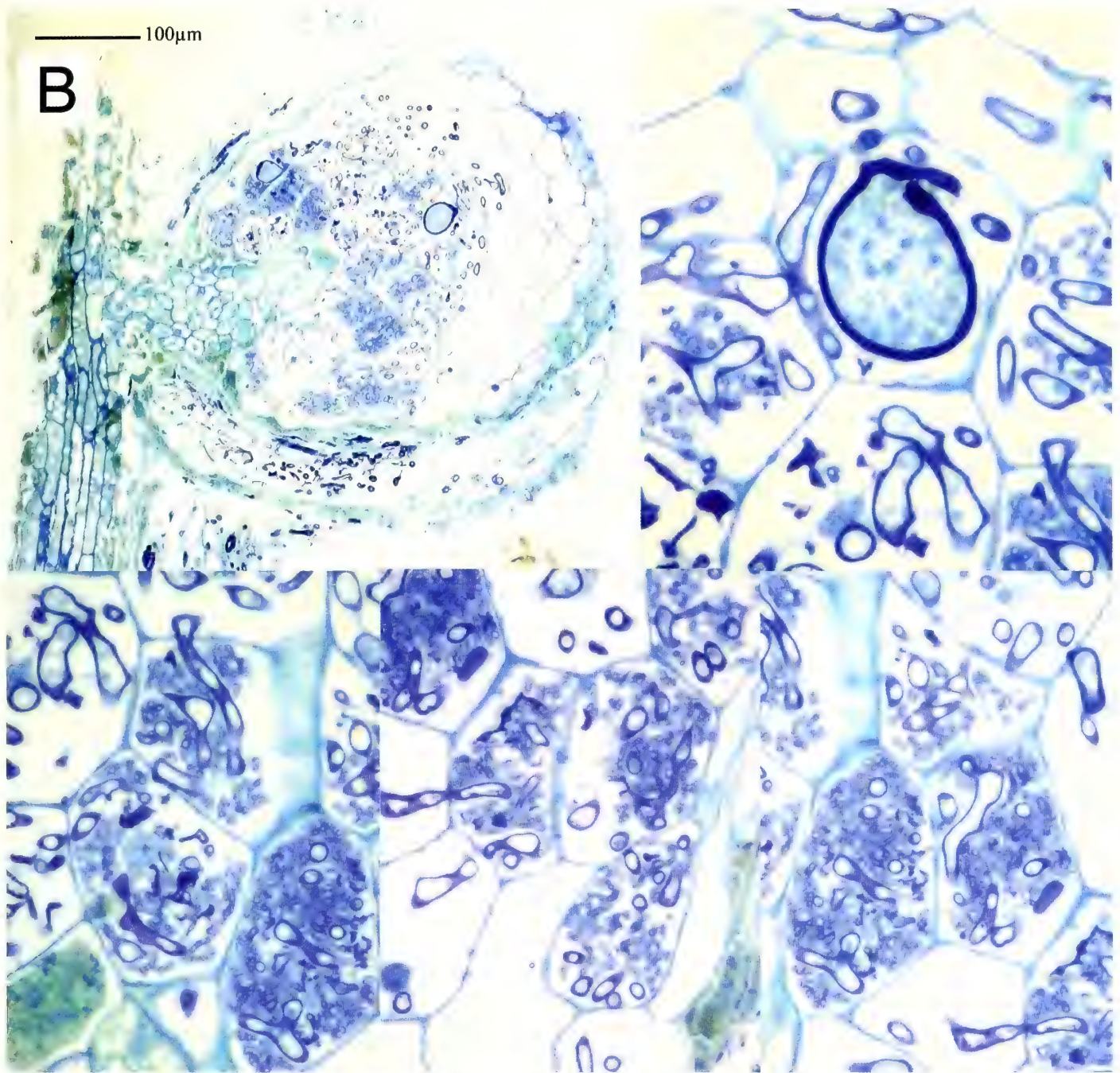


FIGURE 11.4. Internal structure of nodules from (A, facing page) *Podocarpus totara* and (B, above) *Dacrydium cupressinum* showing arbuscular mycorrhizal fungal tissue inside plant root cortical cells, with abundant arbusculate fungal coils (darker blue, fine structures within plant cells) and probable vesicles (ovoid structure in B) and spore (round structure in A). Microscopy was courtesy of Larry Peterson and Lewis Melville from material collected by the authors. Roots were stored in 2.5% glutaraldehyde in PO_4 buffer, pH 6.8, dehydrated in a graded series of ethanol to 100%, embedded in LR White resin (London Resin Company), sectioned (approximately 1–1.5 μm thickness) with glass knives, heat fixed to glass slides, stained with 0.05% toluidine blue O in 1.0% sodium borate, rinsed with water, air dried, and mounted in immersion oil under a cover glass.

have been described as abundant in some nodule root cells (Russell et al., 2002). Although fungi may, in other plants, reinfect a previously infected cell with collapsed arbuscules, this is generally rare (Smith and Read, 2008). By either shedding or apically expanding nodules, podocarps may reestablish the symbiosis, without requiring growth of extensive roots. Second, nodule starch reserves rapidly decline during arbuscular mycorrhizal fungal infection (Russell et al., 2002). The reformation of nodules may be necessary to replenish these reserves. Finally, the thickening of epidermal cell walls in mature nodules is likely to prevent infection by new fungal hyphae (combined with a decline in established infection). If there were any nonsymbiotic mineral nutrient uptake by nodules, this would also be restricted by epidermal wall thickening. Further work is needed to better understand the role of nodule senescence in podocarp mineral nutrient uptake efficiency.

FUNCTIONAL SIGNIFICANCE OF NODULES

The extensive mycorrhizal structures found in podocarp nodules suggest a link between these nodules and arbuscular mycorrhiza, but given that the formation of nodules is neither necessary for mycorrhizal infection nor dependent on mycorrhizal infection to occur, this link must be indirect. Perhaps the simplest hypothesis is that nodules simply permit a plant to increase its extent of arbuscular mycorrhizal infection while minimizing the cost that would be associated with developing an extensive root system (McGee et al., 1999). This hypothesis is supported by the very high levels of mycorrhizal infection often observed in podocarp roots and the frequent occurrence of podocarps on infertile soils, where extensive mycorrhizal development is likely to be beneficial.

Using *Prumnopitys ferruginea* as a model root system, we calculated the root surface area and volume associated with long roots, root hairs, and root nodules. On the basis of 30 segments of root examined, root diameters averaged 0.72 mm (± 0.03 standard error); there were 88 (± 16) root hairs per mm of root, with an average length of 0.78 mm (± 0.02) and a root hair diameter of 0.02 mm. Average volume per nodule was 0.60 mm³ (± 0.03), and there was an average of 0.77 (± 0.06) nodules per mm of root. On the basis of these measurements, the presence of root nodules permits the plant to increase total root volume by around 126% ($\pm 15\%$). Similar results were found for *Dacrydium cupressinum* (except that root hairs were absent), where the presence of root nodules permits the plant to increase total root volume by around 96% ($\pm 10\%$).

Thus, by forming nodules podocarps effectively double their root volume, permitting a much greater extent of

arbuscular mycorrhizal infection than would be possible without nodules. The form of nodules is ideally suited for this purpose—a sphere creates the greatest possible increase in cortex volume at the lowest possible investment in vascular or epidermal tissue.

The economic analogy may be furthered by the observation that some podocarps shed their nodules while retaining long roots. If shedding nodules is physiologically necessary to maintaining mycorrhizal symbioses, then plants may minimize costs by forming very short roots with maximal volume. Where root hairs form on the nodule epidermis, the reformation of nodules with young epidermal cells may also permit plants to reestablish root hair growth (Figure 11.1b).

Further understanding of the mineral nutrient economy of podocarp nodules might benefit from comparison with the determinate, branching roots typical of ectomycorrhizal plants. The majority of ectomycorrhizal plants have heterorhizic roots, responding to fungal infection by branching or bifurcation of short, generally determinate roots. Although the function of this branching has not been widely evaluated, it seems logical to assume that localized root branching permits a greater volume of interaction between the plant and fungal symbionts and may be analogous to the development of nodules infected by arbuscular mycorrhizal fungi in podocarps. It would be particularly interesting to examine the formation of Y-shaped bifurcated ectomycorrhizal short roots in the Pinaceae (Preston, 1943) to determine whether this process is under the same genetic and physiological controls in the Pinaceae as nodule formation in podocarps. A part of this analysis should question why nodules and bifurcated roots are well developed in gymnosperms but not in angiosperms and whether this reflects other constraints on root morphology, including physiological limits on minimum root diameters in gymnosperms.

OTHER NUTRIENT ACQUISITION STRATEGIES IN PODOCARPS

The most unusual nutrient acquisition strategy within the podocarps occurs in *Parasitaxus usta* (Feild and Brodribb, 2005). Endemic to New Caledonia, *Parasitaxus* is parasitic on *Falcatifolium taxoides* (also Podocarpaceae) and is apparently the only parasitic gymnosperm. Water relations of *Parasitaxus* are similar to parasitic woody plants (e.g., mistletoe), but significantly enriched carbon-13 relative to plant host and the presence of abundant fungal hyphae suggest that photosynthate parasitism involves a fungal partner (Feild and Brodribb, 2005). Thus,

Parasitaxus may be simultaneously a direct and an indirect parasite for different resources.

SYNTHESIS AND CONCLUSIONS

The importance of leaf form in the success of podocarps on infertile soils has long been recognized, yet the importance of root form (particularly nodules) has remained enigmatic. On the basis of the best available evidence we suggest that podocarps do not differ in root function from other plants, at least not in any fundamental way. Evidence for nitrogen fixation or novel fungal associations is weak at best. Instead of invoking some unique *function* of podocarp roots, we suggest that the unique *form* of podocarp roots is itself key to understanding their mineral nutrient uptake strategies. Nodules on podocarp roots greatly increase root volume available for symbiotic interaction with mycorrhizal fungi at minimal cost and therefore maximize mineral nutrient acquisition efficiency. This may be further augmented by the ability of some podocarps to shed and re-form nodules, reestablishing the mycorrhizal symbiosis at minimal root construction cost. Nonetheless, this view must be taken as a hypothesis to be tested.

Despite their root and leaf adaptations, podocarps may not be the best adapted species for the environments in which they occur. Low-nutrient soils, especially those with an accumulation of organic matter, often favor ectomycorrhizal trees (Lambers et al., 2008). Although the arbuscular mycorrhizal associations of podocarps are efficient in the uptake of inorganic phosphate, ectomycorrhizal fungi have much greater capabilities for organic nutrient capture (Lambers et al., 2008). Where present, ectomycorrhizal trees may therefore gradually displace podocarps and other arbuscular mycorrhizal vegetation (Taylor et al., 2009). This process may be contributing to the gradual displacement of podocarp forests by ectomycorrhizal *Nothofagus* in New Zealand (McGlone et al., 1996) and ectomycorrhizal *Quercus* in alpine South America (Van't Veer and Hooghiemstra, 2000). Podocarps have a significant advantage over ectomycorrhizal vegetation, however, as they share arbuscular mycorrhizal fungi with many other plant species, whereas the spread of ectomycorrhizal trees may be slowed by a lack of compatible mycorrhizal symbionts (Baylis, 1980; Dickie and Reich, 2005).

Progress on understanding the mineral nutrient acquisition of podocarps has been slow, partially because of an apparent fixation (pun intended) on nodules and the possibility of nitrogen fixation. We suggest that further research would be aided by (1) an economic perspective on

carbon costs and mineral nutrient efficiency of root and nodule formation in the podocarps, including any physiological constraints limiting alternative strategies such as increased specific root length, (2) an investigation into the genetic basis for nodule formation, testing whether this trait is homologous with ectomycorrhizal short roots in the Pinaceae, and (3) understanding the co-occurrence and replacement of podocarps by ectomycorrhizal trees and the implications of this for ecosystem processes.

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Podocarpaceae in Tropical Forests: A Synthesis

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The Podocarpaceae comprises 18 genera and about 173 species of evergreen, coniferous trees and shrubs. It is the most successful gymnosperm family in angiosperm-dominated tropical forests (Brodribb, this volume). Podocarps are distributed mainly in the Southern Hemisphere, with populations also extending as far north as China and Japan and to Mexico and the Caribbean in the neotropics (Dalling et al., this volume; Enright and Jaffré, this volume; Adie and Lawes, this volume).

Molecular and fossil evidence suggests that the Podocarpaceae originated during the Triassic–Jurassic in Gondwana (Biffin et al., this volume; Morley, this volume). Currently, the greatest generic diversity of the Podocarpaceae is in Malesia (Enright and Jaffré, this volume). Podocarps did not migrate into tropical latitudes until later in their evolutionary history, appearing for the first time in Southeast Asia during the late Eocene, probably dispersing via the Indian Plate (Morley, this volume). Thus, the present latitudinal distributions have emerged in Asia and Africa over the last 40 million years. Although extinction rates in general appear to have been high within the family, a major shift in diversification rate is estimated to have taken place in the mid- to Late Cretaceous and Paleocene, with most extant genera becoming established in Gondwana

during this period. This shift could reflect reduced extinction and/or increased speciation in response to the expansion of angiosperm-dominated tropical forests (Biffin et al., this volume). An alternative explanation for the Late Cretaceous and Paleocene diversification could be the onset of wetter and warmer climatic conditions associated with the opening of the Southern Ocean (Morley, this volume).

Some podocarp taxa show widespread and/or disjunct distributions. In the absence of molecular data, it is difficult to infer migration patterns or the potential for gene flow among these disjunct populations. Patterns of relatedness among populations in tropical forests could help reveal whether current populations are relicts of cooler tropical climates associated with the Last Glacial Maximum or the consequence of postglacial occupancy of suitable habitat.

Tropical podocarps are most abundant in mid- to high-elevation forests, suggesting that the habitat requirements of temperate ancestors have been retained as podocarps radiated into the tropics. Podocarps also occur occasionally in lowland tropical rainforest, but this is the exception, rather than the rule (Dalling et al., this volume; Enright and Jaffré, this volume; Adie and Lawes, this volume; Coomes and Bellingham, this volume). One such exception is their prominence in lowland heath forests (kerangas) on Borneo (Enright and Jaffré, this volume). Thus, in Asia, podocarp taxa have apparently dispersed through both lowland and montane habitats. For example, the dispersal pathway for *Dacrydium* appears to have been via India through kerangas, i.e., heath forests growing on acidic, sandy soils that are low in nutrients, during the Paleogene. On the other hand, *Dacrycarpus* and *Phyllocladus* appear to have jumped between islands of montane/alpine habitat via New Guinea at the time of Plio–Pleistocene global cooling (Morley, this volume; Enright and Jaffré, this volume). A similar pattern of distributions can also be found in the neotropics, where podocarps are mainly montane, but with notable lowland exceptions (Dalling et al., this volume). There, podocarps are absent from most of the Amazon lowlands, except for the white sands around Iquitos, Peru, and nutrient-poor soils of the Guyana Shield. However, podocarps do occur at sea level on islands off both the Pacific and Atlantic coasts of Central America. It should also be noted that podocarp pollen was relatively common in lake sediments from the Amazon lowlands during the Last Glacial Maximum approximately 18,000 years ago but decreased to trace amounts during the Holocene, presumably as a result of climate warming (Colinvaux et al., 1996).

Given that podocarps in lowland tropical forests appear to achieve their highest abundance on low-fertility soils (Dalling et al., this volume; Enright and Jaffré, this volume; Coomes and Bellingham, this volume), do they have high nutrient use efficiency and/or unique mechanisms for acquiring nutrients? Nutrient use efficiency can be defined as the product of nutrient productivity and mean nutrient residence time (Berendse and Aerts, 1987; Aerts and Chapin, 2000). Nutrient productivity is a rate variable, expressed as carbon uptake per unit of nutrient per unit time. Mean nutrient residence time is the average amount of time that a unit of nutrient spends in the plant between acquisition from the environment and loss through above- and below-ground litter production. Leaf-level measurements suggest that podocarps do not have nutrient productivities that can match those of tropical angiosperms. In a comparison of conifer and angiosperm seedlings grown in Panama, *Podocarpus guatemalensis* had photosynthetic nitrogen productivity of $38 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$, whereas mean values were 64 and $162 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$ for three other conifer species and 11 angiosperm species, respectively (Cernusak et al., 2008). Mean values for photosynthetic phosphorus productivity were 0.5, 0.7, and $2.5 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ P s}^{-1}$ for *P. guatemalensis*, three other conifer species, and 11 angiosperm species, respectively. In general, podocarps have low photosynthetic rates per unit leaf mass compared to angiosperms, in common with other conifer taxa (Lusk, this volume). Low mass-based photosynthetic rates contribute to low leaf-level nutrient productivities (Aerts and Chapin, 2000).

It seems likely, therefore, that any advantage that tropical podocarps have in terms of nutrient use efficiency should derive from mean nutrient residence time, rather than from nutrient productivity. Mean nutrient residence time can vary as a function of leaf and root life spans, tissue nutrient concentrations, and the efficiency of nutrient resorption from senescing tissues. In common with other conifers, podocarps do tend to have long leaf life spans compared to angiosperms (Lusk, this volume). Podocarps can also have lower leaf nutrient concentrations than angiosperms: *P. guatemalensis* had leaf nitrogen and phosphorus concentrations of 1.5% and 2.5‰, respectively, compared with values of 1.2% and 2.9‰ for three other conifer species and 1.7% and 3.1‰ for 11 angiosperm species grown under similar soil conditions in Panama (Cernusak et al., 2008). Similarly, *Podocarpus urbanii* also had lower leaf nitrogen and phosphorus concentrations than co-occurring angiosperms in Jamaica (Dalling et al., this volume), but on Mount Kinabalu in Borneo nitrogen and

phosphorus concentrations in the phyllodes of *Phyllocladus hypophyllus* were not different from those in leaves of co-occurring angiosperms (Kitayama et al., 2004). More data are therefore needed to determine whether leaf nutrient concentrations in tropical podocarps tend, in general, to be lower than in co-occurring angiosperm trees. There are no data that we are aware of for nutrient resorption efficiency from senescent leaves of tropical podocarps. Nor are we aware of data for root life spans, root nutrient concentrations, or resorption efficiency from senescing roots. Thus, although it is likely that tropical podocarps will have longer mean nutrient residence times than tropical angiosperms, the evidence currently available is insufficient to demonstrate this conclusively.

In response to the second part of the question posed above, podocarps do not appear to possess any unique mechanism for acquiring nutrients. They do have conspicuous nodules on their roots that grow in the absence of fungi or bacteria; their function remains unclear, although they appear to play no significant role in atmospheric nitrogen fixation. Podocarp roots show very high rates of infection by arbuscular mycorrhizal fungi in both long and short nodular roots (Dickie and Holdaway, this volume). Thus, the nodules may simply serve to increase root volume for interaction with symbiotic mycorrhizal fungi. Dickie and Holdaway (this volume) argue that the nodules could minimize root construction and turnover costs while maximizing the root volume available to support mycorrhizal associations. On the basis of measurements on Mount Kinabalu, Borneo, Kitayama et al. (this volume) further suggest that podocarps may form loose symbiotic associations with soil microbial communities.

In summary, there does not appear to be a single, outstanding feature that can explain why podocarps are relatively most successful on infertile soils in lowland tropical forests. The explanation may rather lie in a suite of traits that combine to enable podocarps to compete successfully when the productivity advantage of angiosperms is diminished by nutrient poverty (Brodribb and Feild, 2010). Some possible examples of such traits are long mean nutrient residence times associated with long leaf and root life spans and low tissue nutrient concentrations, efficient manipulation of mycorrhizal symbioses, and some degree of control over the composition of soil microbial communities by root exudates and the quality and quantity of leaf litter (Kitayama et al., this volume).

Despite the frequent association of tropical podocarps with low-nutrient soils, it would be incorrect to assume that they are strictly confined to those soils. Broad-leaved podocarps, in particular, can also occur on more

productive sites. This may be because broad leaves are important for light interception efficiency and competitiveness with co-occurring angiosperms at nutrient-rich sites, where dense canopies cast a pronounced shadow over regenerating seedlings (Adie and Lawes, this volume). Broad-leaved podocarps tend to be faster growing and shorter lived and have shorter leaf longevity and higher leaf litter quality than imbricate-leaved genera (Enright and Jaffré, this volume). These traits in broad-leaved podocarps may approach those of co-occurring angiosperms. Under African forest conditions, superior shade tolerance by broad-leaved podocarps allows them to dominate competing angiosperms over a range of soil nutrient conditions (Adie and Lawes, 2009). Phylogenetic analyses suggest that the broad-leaved podocarps may have a higher diversification rate than genera with imbricate leaves (Biffin et al., this volume), possibly linked to differences between the two groups in metabolic rates.

The ability to produce flattened, plagiotrophic leaves and shoots is fundamental to the success of podocarps in competition for light with angiosperms. Leaf flattening is a prominent feature within the Podocarpaceae and distinguishes the broad-leaved podocarps from most other conifer taxa. Flattened leaves are likely to be a key factor enabling shade tolerance of podocarps (Brodribb, this volume). The flattened leaves contain sclereids, which increase water transport from the leaf midvein to the sites of evaporation in the leaf lamina. Freed from the temperate-zone constraint of freezing, tropical broad-leaved podocarps can increase leaf size and thus have converged upon a strategy of leaf architecture that resembles that of co-occurring angiosperms. Whereas temperate podocarps tend to have lower leaf area ratios than co-occurring angiosperms, tropical podocarps may be more able to emulate shade-tolerant tropical angiosperms and intercept sunlight with a similar efficiency.

In general, podocarps do not tolerate drought. This may be because they possess wood that is vulnerable to embolism by water stress and are unable to refill embolized tracheids (Brodribb, this volume). Additionally, the vascular system associated with homoxylous conifer wood may be insufficient to supply water to the relatively large leaf area carried by broad-leaved podocarps under conditions of high evaporative demand and/or low soil water potential. This may lead to excessively low leaf water potentials and sharply curtailed photosynthetic rates under such conditions. An extreme exception to the general intolerance to drought among podocarps occurs in the Mediterranean-type climate of southwest Australia. There, *Podocarpus drouynianus* forms a lignotuber that allows it

to resprout following shoot dieback caused by fire and/or drought (Ladd and Enright, this volume). Kerangas forests are also subject to occasional drought, and species growing in them, including podocarps, show an array of leaf traits, in combination with reduced plant size, that reduce water loss (Enright and Jaffré, this volume).

Podocarps are long-lived in the temperate zone, and there is evidence that they also have a longevity advantage over competing angiosperms in the tropics (Kitayama et al., this volume). They are often subcanopy components and not emergent in tropical forests, unlike many New Zealand podocarps (Coomes and Bellingham, this volume). Landscape-scale disturbance is probably not necessary for regeneration of tropical podocarps, even though many species occur in areas where disturbances such as cyclones and landslides are common. Tropical podocarps are fire intolerant. In general, podocarp seedlings show low abundance. Thus, in many cases, slow growth and high persistence likely facilitate their ultimate recruitment to the canopy. Little is known about herbivory in tropical podocarps or their defenses against herbivores. Similarly, pollination and seed dispersal in tropical podocarps have been little studied.

CONSERVATION, MANAGEMENT, AND GLOBAL CHANGE

In common with most tropical trees, the immediate threat to tropical podocarps is deforestation associated with timber extraction, mining, and other modern anthropogenic activities, including drainage of peat swamps and expansion of agricultural activities onto poor soils. Several podocarps are local montane endemics, and these may be further threatened by shifting climatic zones associated with global climate change and deforestation (Walther, 2004; Jump et al., 2009). These species could become increasingly rare within narrowing altitudinal bands, particularly on islands and mountains. Tropical podocarps are fire and drought intolerant, so they will be particularly adversely affected wherever climate change leads to hotter, drier conditions with more frequent fires.

Although podocarp timber has many uses for human activities, their slow growth rates make their exploitation ecologically unsustainable. Therefore, continued harvesting of existing individuals from natural stands threatens populations (Lawes et al., 2007).

Habitat specialization restricts the potential area of suitable sites for podocarps, which requires broad-scale habitat conservation to capture potential conservation sites. The association with unusually infertile soils is also

significant with regard to podocarp conservation. International Union for Conservation of Nature (IUCN) assessments of species conservation status are effectively determined by range sizes, in the absence of data on population number or population change. Many podocarps have large ranges (i.e., thousands of square kilometers) but probably only occupy a fraction of that area. Thus, if podocarps really are restricted to unusual habitats, then they may be more endangered than current assessments suggest. Additionally, if conservation priorities are defined by phylogenetic diversity, podocarps have a high conservation value because their nearest living sister taxa are separated by about 250 million years (Biffin et al., this volume).

A summary of tropical podocarp species that are threatened based on assessments in the 2009 IUCN Red List of Threatened Species (IUCN, 2009) is provided in Table 12.1. In addition to these species, a number of taxa are also considered “near threatened” or “data deficient.” Thus, Table 12.1 likely represents a conservative estimate of the true number of tropical podocarp species currently under threat of extinction. Taking this conservative estimate, roughly one-fourth of tropical podocarp species are threatened, with five species considered critically endangered, 18 species endangered, and 16 species vulnerable (Table 12.1). Many of the species in Table 12.1 are island endemics, including four species from Madagascar, six species from New Caledonia, and seven species from Borneo. In addition, there are a number of species endemic to islands in the Western Pacific and the Caribbean.

Because podocarp-dominated forests are often associated with ecosystems that have poor drainage and large accumulations of organic material on the forest floor, they play an important role in carbon storage. Leaf and litter characteristics of podocarps generally result in slow decomposition rates, leading to an accumulation of carbon in the litter layer and in the soil. This carbon can be rapidly lost when podocarp-dominated forests are cleared for other land uses (Freier et al., 2010). Thus, the UN global initiative to reduce emissions from tropical deforestation and degradation should place a high value on podocarp-dominated forests.

RECOMMENDATIONS FOR FUTURE RESEARCH

Podocarps are potentially good indicators of environmental change over their 250 million year history. Important aspects of the phylogeny of Podocarpaceae remain to

TABLE 12.1. Conservation status of threatened tropical species of the Podocarpaceae (IUCN, 2009). Abbreviations: CR, critically endangered; EN, endangered; VU, vulnerable.

Species	Status	Location	Habitat
<i>Acropyle sabniana</i>	CR	Fiji	Montane forest
<i>Afrocarpus mannii</i>	VU	São Tomé, Gulf of Guinea	Montane forest
<i>A. usambarensis</i>	VU	East African highlands	Montane forest
<i>Dacrydium comosum</i>	EN	Malay Peninsula	Montane Forest
<i>D. ericoides</i>	VU	Sarawak, Borneo	Hill forest, ultrabasic
<i>D. gracile</i>	VU	Sabah, Borneo	Montane forest
<i>D. guillauminii</i>	CR	New Caledonia	Riparian
<i>D. leptophyllum</i>	VU	Irian Jaya	Montane heath forest
<i>D. nausoriense</i>	EN	Fiji	Montane rainforest
<i>Falcatifolium angustum</i>	VU	Sarawak, Borneo	Lowland rainforest
<i>Nageia maxima</i>	VU	Sarawak, Borneo	Peat swamp forest
<i>Parasitaxus usta</i>	VU	New Caledonia	Montane rainforest understory
<i>Podocarpus affinis</i>	VU	Fiji	Montane rainforest
<i>P. angustifolius</i>	EN	Cuba	Montane rainforest
<i>P. aristulatus</i>	VU	Cuba, Hispaniola	Montane forest
<i>P. beecherae</i>	EN	New Caledonia	Wet maquis
<i>P. brevifolius</i>	VU	Sabah, Mount Kinabalu	Montane forest
<i>P. capuronii</i>	EN	Madagascar	Montane forest
<i>P. costalis</i>	EN	Philippines, Taiwan	Montane forest
<i>P. costaricensis</i>	VU	Costa Rica	Lowland to montane forest
<i>P. decumbens</i>	CR	New Caledonia	Montane stunted forest
<i>P. deflexus</i>	EN	Malay Peninsula, Sumatra	Montane forest
<i>P. gibbsii</i>	VU	Sabah, Mount Kinabalu	Montane forest
<i>P. globulus</i>	EN	Sabah, Borneo	Lowland to montane forest
<i>P. hispaniolensis</i>	EN	Dominican Republic	Montane forest
<i>P. humbertii</i>	EN	Madagascar	Montane forest, heath
<i>P. laubenfelsii</i>	EN	Sarawak, Borneo	Kerangas, montane heath
<i>P. longifoliolatus</i>	EN	New Caledonia	Montane rainforest understory
<i>P. lophatus</i>	VU	Philippines	Montane forest
<i>P. nakaii</i>	EN	Taiwan	Subtropical forest
<i>P. palawanensis</i>	CR	Philippines	Lowland rainforest
<i>P. pallidus</i>	VU	Tonga	Montane forest
<i>P. pendulifolius</i>	EN	Venezuela	Montane rainforest
<i>P. perrieri</i>	CR	Madagascar	Montane forest
<i>P. polyspermus</i>	EN	New Caledonia	Montane forest
<i>P. purdieanus</i>	EN	Jamaica	Montane forest
<i>P. rostratus</i>	EN	Madagascar	Montane forest
<i>Retrophyllum minus</i>	EN	New Caledonia	Riparian
<i>R. rospigliosi</i>	VU	Venezuela, Colombia, Peru	Montane forest

be resolved, and more and better information would aid their use as environmental indicators. A phylogeographic perspective could help in understanding population connectivity under changing climate in the Holocene.

Dispersal and recruitment dynamics of infrequent lowland tropical podocarps are largely unknown. As

podocarps are mostly dispersed by large-bodied animals, local extinction of dispersers may particularly impact upon podocarp regeneration and recruitment and genetic diversity, especially on islands. Population genetic data could effectively address issues of pollen and seed dispersal, genetic diversity, and relatedness.

Podocarps colonize second-growth forests in some temperate regions. The potential for podocarps to colonize second-growth tropical forests, which are increasing in area in some tropical regions, is unknown. Physiological and growth responses of podocarps to variation in atmospheric CO₂ concentration are unknown but could have important implications for their use as indicators of environmental change.

Understanding why tropical podocarps are mostly restricted to wet, infertile environments requires information about their ecophysiology. For example, seedling leaf area ratios of temperate podocarps are generally low relative to co-occurring angiosperms, but virtually nothing is known of leaf area ratios of large-leaved lowland tropical podocarps. More information about physiological mechanisms of drought sensitivity, including stomatal function and susceptibility to cavitation, is key to understanding current podocarp distributions. The physiological adaptations allowing podocarp success on infertile soils, potentially including conspicuous root nodules, mycorrhizal symbioses, and nutrient retention strategies, are key areas for further research. A better understanding of podocarp ecophysiology is likely to be achieved through integrated, whole-plant studies, rather than by addressing nutrient, carbon, and water relations independently of each other.

Finally, podocarps are poorly represented in permanent census plots in tropical forests, which limits knowledge of demography and habitat associations. Important demographic factors and environmental drivers are likely to be longevity, relative shade tolerance, and edaphic properties. Permanent plot data could provide an opportunity to collate such information. Results could provide a framework to inform decisions about silviculture and forest management of podocarps.

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Subject Index

Page numbers followed by “t” refer to a table; page numbers followed by “f” refer to a figure.

- accessory transfusion tissue, 167, 168f, 169, 171f
- acid phosphatase activity, 111–115
- Africa, 21, 79–80, 94–95, 190
 - and coastal forests, 92–94
 - and drought resistance, 129
 - ecology of, 86–88
 - endangered species in, 193t
 - fossil record from, 24–26, 27f, 35, 36
 - and podocarp ecophysiology, 85–86
 - and regeneration, 89–90, 94, 127
 - role of disturbance in, 88–89
 - and seed dispersal, 152, 158
 - and soil nutrients, 90–92
 - and species dispersal, 30, 35–36, 38
 - species distribution in, 81–85, 189
 - species diversity in, 22, 80–81
- altitudinal range, 61–63, 66, 102–106
- Amazonia
 - and species dispersal, 129
 - species distribution in, 44, 47f, 48
 - species of, 136
- Andes
 - fossil record from, 44
 - and species dispersal, 38, 129
 - species distribution in, 45, 48, 54, 131
 - species of, 136, 137
- angiosperms, 60, 63, 94, 131
 - and acid phosphatase activity, 112
 - advantages of, 70, 158
 - and arbuscular mycorrhizal fungi, 122
 - and cold temperatures, 121–122
 - and competitive advantages of podocarps in Malesia, 68
 - constraints on, 80
 - and gap-phase dynamics, 88
 - growth of, 68

- angiosperms (*continued*)
 impact of climatic fluctuation on, 94–95
 impact on dispersal, 36
 leaf to stem ratio of, 68
 longevity of, 70
 in *Podocarpus*-dominated forests, 87–89
 pollen record of, 27f
 regeneration of, 80, 90
 and seedling growth, 46
 and shade, 87, 108–109
 vessels of, 85–86, 159
- animal dispersal
 of seeds, 69, 146, 151, 152, 158, 193
- Antarctica, 22, 36
- antiherbivore defenses, 63
- arbuscular mycorrhizal fungi, 63, 91–92, 178t, 185
 and angiosperms, 122
 and lipid abundance, 114t
 and root nodule, 181, 183f, 184
 and roots, 176–177, 179, 180f, 191
- Argentina, 136
- Asia
 endangered species in, 61
 fossil record from, 22, 23t, 24, 26, 28, 31, 32
 and species dispersal, 26, 28–31, 36, 38f, 172, 189–190
 species distribution in, 33, 60, 102, 129, 142
- Assam, 72–75t
- Australasia, 21
 fossil record from, 28, 36
 and species dispersal, 30
 species distribution in, 131
 species diversity in, 129
- Australia, 70, 71t
 extinction in, 131, 169, 170, 171f
 fire-tolerant podocarps in, 141, 142, 143t, 146–148, 150f, 151–154
 fossil record from, 22, 30, 33–36, 129, 151
 impact of drought intolerance in, 17
 and poor soil, 122
 range contraction in, 2, 169, 170
 and resprouting after fire, 128
 seed dispersal by animals in, 69
 and species dispersal, 31f, 33, 36, 38
 species distribution in, 60–62, 151
 species diversity in, 59–60, 72–75t
 species of, 134–136
- Banka Island, 133
- Bayesian method, 2, 4, 7
- biogeography, 81–85
- birth-death model, 10, 12, 14f
- Bolivia, 45, 54, 136
- Borneo, 71t
 altitudinal range in, 102–106
 endangered species in, 192, 193t
 and podocarp adaptations, 109–114, 190–191
 and population ecology, 108–109
 soil types in, 106–108
 and species dispersal, 33–36, 38
 species distribution in, 58f, 60–63, 130–131, 190
 species diversity in, 59, 60, 72–75t
 species of, 132–136
- Brazil
 fossil record from, 44
 species distribution in, 49t, 68–69, 71
 species of, 136
- bryophytes, 62
- Burma, 59t, 72–75t, 133, 135, 136
- calcium, 67
- Cambodia, 59t, 72–75t, 133
- canopy, 128
 architecture of, 124–125, 130, 131
 and gap-phase dynamics, 88–89
- Celebes, 132–136
- census plot, 62
- China, 2
 fossil record from, 22, 28, 31
 and species dispersal, 31, 36
 species distribution in, 61, 189
 species of, 59t, 72–75t, 132, 133, 135, 136
- chloroplast
 divergence estimated using, 9, 11f, 12f
 generic schemes confirmed by, 4
- climate
 fluctuations in, 66, 94–95
 impact of on dispersal, 31, 33, 36, 37f, 38
 impact of on diversity, 59–60
- climate change, 68, 190, 192
- cloud forest, 61, 68, 69, 102, 105–106
- coastal forest, 92–95
 as habitat, 22, 28, 45, 81, 86, 151
- Colombia
 conservation issues in, 54
 species distribution in, 44, 45, 48, 49t, 50, 54
 species of, 136
 vulnerable species in, 193t
- conduit diameter, 158–160
- conifers, 26, 28, 159
 advantages of, 158
 and angiosperm competition, 2, 60
- conservation, 54, 61, 192, 193t
- construction
 as threat, 68
- Costa Rica, 45, 49t, 136, 193t
- Cuba
 endangered species in, 193t
 and species dispersal, 172
 species distribution in, 45, 46, 50, 54
- “Dacrydioid” clade, 7
- diameter, stem, 50, 51, 52f
 and conduit diameter, 160f
 and growth rate, 63, 70, 71t
- diameter, tree
 growth rate of, 52, 54, 120
- diameter at breast height (dbh), 106f, 108–110f
 in canopy gaps, 88
 and median crown position index, 112f
 in mountain forests, 61
 and soil type, 104t
 and tree height, 111, 112f
- diversification
 patterns of, 10, 12–13
 rates of, 3, 14–15, 16f, 17, 189–190
- Dominican Republic, 131, 193t
- drought, 68, 89
 adaptations to, 63
 intolerance to, 17, 122, 169–170, 191, 192
 resistance to, 170–171
- ecophysiology, 2, 17, 70, 85–86, 194
 and seedlings, 68, 72
- ectomycorrhizal fungi, 111, 122, 179, 184–185
- Ecuador, 44, 45, 49–50, 54
- embolism, 63, 122
 in cold climates, 86, 171–172
 and conduit diameter, 159–160
 and drought, 191
- endangered species, 61
- environmental indicators
 Podocarpaceae as, 192–194
- erosion, 61
- evolution, 72
 and drought resistance, 63
 of leaves, 63, 68, 166–167, 169, 191–192
 and poor soil, 67, 129
 rates of, 2
 and shade tolerance, 128–129
- extinction rate, 12–14, 15f, 189–190
- Fiji
 endangered species in, 193t
 species of, 59t, 61, 72–75t, 132–133, 135
- fire, 153
 impact on distribution, 67, 68, 84, 86, 89
 impact on diversity, 60
 intolerance to, 17, 45–46, 128, 131, 192

- and resprouting, 128, 147
- and seed production, 143, 145–146
- fossil record, 2, 9–10, 13
 - pollen in, 22–28, 30–31, 33–36, 44, 80, 83–84, 190
- fragmentation
 - as threat, 68, 69
- general time reversible model, 4
- Gondwana
 - Podocarpaceae originating in, 21–22, 35, 44, 102, 169, 189–190
 - species distribution from, 81
 - species diversification in, 36
- growth rate, 71t, 120
 - as insufficient to survive, 127
 - and light, 90–91, 108–109, 124f
 - and median crown position, 111f
 - and nutrients, 50, 90–91, 124f
 - of seedlings, 68, 120
- Guatemala, 137
- Guyana, 137
- habitat, 60, 121, 190
 - cloud forest as, 61, 69, 102, 105–106
 - coastal forest as, 22, 28, 45, 81, 86, 151
 - heath forest as, 60, 61, 190
 - lowland forest as, 45, 61, 190
 - montane forest as, 60, 61, 190
 - in neotropics, 46–50
 - peat forest as, 60, 61
 - tropical rainforest as, 132–137, 159, 165–166, 190
- Haita, 49t
- heath forest, 60–63, 190
- height, 112t, 130t
- Hispaniola, 45–46, 49t, 54, 193t
- humans
 - as threat, 67–69
- hydraulic function
 - in cold climates, 159, 171–172
 - and drought, 170–171
 - and leaf structure, 68, 167, 169
 - and light conditions, 60
 - and tracheids, 86, 120, 122
- India, 21–22
 - fossil record from, 25, 26, 36
 - and species dispersal, 28, 30, 35–36, 189–190
 - species distribution in, 57, 58f, 59t, 61, 72–75t
 - species diversity in, 60, 72–75t
 - species of, 132–133
- Indochina, 24–25, 33, 133
- Indonesia
 - fossil record from, 35
 - and species dispersal, 31f
- species distribution in, 58f, 60
- species of, 132–133, 136
- International Union for Conservation of Nature, 192, 193t
- Irian Jaya, 35, 193t
- Jamaica
 - endangered species in, 193t
 - Podocarpus urbanii* in, 50–54, 130, 190
 - species distribution in, 45, 49t, 50
 - species of, 134–135
- Japan, 2, 69, 189
 - podocarp leaf structure in, 125
 - podocarp longevity in, 123
 - and regeneration after disturbance, 128, 130
 - and species dispersal, 31, 36
 - species distribution in, 58f, 122
 - species of, 133, 136
- Java
 - fossil record from, 23f, 26, 28, 30–33
 - and species dispersal, 36, 38
 - species of, 133, 135, 136
- Laos, 59t, 72–75t, 133, 135
- leaf mass per area, 161
- leaves, 86, 126f, 130t, 131–132
 - adaptations to, 63, 68, 124–125, 128, 165–167, 191–192
 - comparison of between conifers and angiosperms, 159–162
 - flattening of, 2, 17, 191
 - longevity of, 70, 123, 161–162
 - nutrients in, 190–191
 - phylogenetic studies on, 3–4
 - size of, 60, 142, 149, 151, 171
 - structure of, 60, 63, 68
- light
 - and competition with angiosperms, 60, 68, 124
 - and growth, 90–91, 108–109, 124f
 - and hydraulic function, 60
 - and leaf structure, 124–125, 128, 167
 - and photosynthesis, 68
 - and regeneration, 86–88, 92, 94, 126–127
- lignotubers, 146–147, 152–153
- logging, 54, 61, 68, 69, 93–95, 192
- longevity
 - of leaves, 70, 123, 161–162
 - of podocarps, 17, 70, 71t, 94, 192
 - of podocarps in Asia, 111, 114, 123
 - of podocarps in New Zealand, 94, 127–129, 131
 - and wood density, 123
- lowland forest, 45, 60–62, 190
- Madagascar, 21
 - endangered species in, 192, 193t
- species diversity in, 80–81
- species of, 137
- magnesium, 67
- Malaya, 59t, 62–63, 72–75t, 132–135
- Malay Peninsula
 - endangered species of, 193t
 - and species dispersal, 33f, 36, 38
 - species of, 133
- Malaysia, 59, 62, 132–133, 135
- Malesia, 21, 57, 70–75t
 - altitudinal range of podocarps in, 61–63
 - ecophysiology of podocarps in, 68
 - obstacles to studying podocarps in, 71–72
 - population ecology in, 68–69
 - and species dispersal, 28, 30
 - species distribution in, 58f, 59t, 60–61, 72–75t
 - species diversity in, 43–44, 57, 58f, 59–60
 - species of, 22, 132, 135
- manganese, 67
- masting, 69
- Mexico, 2, 189
 - species distribution in, 45, 49t, 69
 - species of, 137
- mining, 67, 68, 192
- molecular clock hypothesis, 2
- molecular data, 2–7t, 44
- Moluccas, 59t, 72–75t, 132–135
- montane forest, 45, 60–62, 190
- morphology, 3–4
- mycorrhizal fungi. *See* arbuscular mycorrhizal fungi; ectomycorrhizal fungi
- neotropics
 - altitudinal range of podocarps in, 45–46, 48f
 - conservation concerns in, 54
 - fossil record from, 44
 - habitats in, 46–50
 - species distribution in, 44–45, 49t, 190
 - species diversity in, 43–44
- Nepal, 57
 - species of, 59t, 61, 72–75t, 132–133
- New Britain, 132–133
- New Caledonia, 63, 64–65f, 66–68, 71t
 - and catastrophic regeneration, 131
 - endangered species in, 193t
 - species diversity in, 43, 58f, 59–60, 72–75t
 - species of, 132–135
- New Guinea, 71t
 - and fire, 89
 - fossil record from, 23t, 25, 26, 36, 38
 - seed dispersal in, 69

New Guinea (*continued*)

- and species dispersal, 31f, 33, 34, 36, 38, 190
 - species distribution in, 58f, 60–63, 66, 102, 129–131
 - species diversity in, 59, 72–75t
 - species of, 132–136
- New Hebrides, 132, 135
- New Zealand, 71t
- fossil record from, 33
 - and mycorrhizal infections, 176–177, 185
 - podocarp foliage in, 126f
 - podocarp longevity in, 94, 127–129, 131
 - and regeneration, 89–90, 92, 127–129, 131
 - and role of disturbance, 88–89
 - and seed dispersal, 152
 - and soil quality, 91, 112, 120, 122–124
 - species distribution in, 46, 58f, 121–122, 125, 127
 - species of, 132
- nickel, 67
- nitrogen, 67
- and acid phosphatase activity, 115
 - concentration of, 51
 - efficient use of by conifers, 70
 - fixation of, 112–113, 180–181
 - and growth, 50, 90–91
 - leaf concentration of, 190–191
 - and leaf longevity, 123
 - relationship of to podocarp abundance, 107–108, 110
 - reserves of, 95
- nutrient residence time, 190–191

paleoclimates

- to clarify relationships, 24
- pollen used in reconstruction of, 45, 129

palynological data, 44

Panama, 190

- and regeneration, 131
- species distribution in, 45, 48–50

Patagonia, 21–22

- fossil record from, 28, 30, 33, 35–36
- and species dispersal, 38

peat forest, 31–32, 60–63

Peru

- species distribution in, 45, 49, 54, 190
- species of, 136
- vulnerable species in, 193t

Philippines

- endangered species in, 193t
- and species dispersal, 33
- species distribution in, 58f, 61

- species diversity in, 59, 72–75t
 - species of, 132–136
- phosphorous, 67
- and acid phosphatase activity, 111–112, 114
 - concentration of, 51
 - efficient use of by conifers, 70
 - and growth, 50
 - leaf concentration of, 190–191
 - and leaf longevity, 123
 - relationship of to podocarp abundance, 107–108, 110
- photosynthesis, 70
- and adaptation of flattened leaves, 166–167
 - and canopy architecture, 124–125, 130, 131
 - and drought, 191
 - and leaf life span, 161–162
 - low capacity for, 68, 86, 120
 - and nutrient use, 114, 190
- photosynthetically active radiation, 87, 91f, 92, 124, 125
- phylloclades, 17, 167
- phylogenetic relationships, 2–4, 7, 8f
- “Podocarpoid” clade, 7
- pollen, 34f, 35, 38, 44, 69
- dispersal of, 70–71
 - fossil record of, 22–28, 30–31, 33–36, 44, 80, 83–84, 190
 - and paleoclimate reconstruction, 45, 129
 - types of, 22–24
 - wind dispersal of, 68, 119
- population ecology, 68–69
- potassium, 67
- “Prumnopityoid” clade, 7

rainforest, tropical, 132–137, 159,

165–166, 190

recreational tracks

as threat, 68

recruitment, 53, 69

regeneration, 114, 128–129

- after disturbance, 125, 127–131
- and gap-phase dynamics, 88–89
- and light, 86–88, 92, 94, 126–127
- patterns of, 80, 89–90
- and shade tolerance, 88, 89–90, 125

relaxed-clock method, 2, 7

relaxed molecular clock, 2–3

- resprouting, 63, 152–154, 191–192
- after fire, 128, 147

root hairs, 176, 177f

root nodule, 177–178, 191

- and mycorrhizal fungi, 180f, 181, 183f, 184
- and nitrogen fixation, 180–181
- replacement of, 181, 184

roots

- and acid phosphatase activity, 111–115
- and arbuscular mycorrhizal fungi, 176–177, 179, 180f, 191
- as beaded, 178–180

São Tomé, 81, 84, 193t

saprophytic fungi, 113–114

- sclereids, 166f, 167, 168f, 169, 191
- and cold temperatures, 172
- and drought, 122, 170–171

seedlings

- ecophysiology of, 68, 72
- growth of, 68, 90–91, 120

seeds

- animal dispersal of, 69, 146, 151, 152, 193
 - dispersal of, 69–71, 84–85, 158
 - germination of, 69, 84, 142, 143, 145f
 - production of, 69, 143, 145–146
- shade tolerance, 71t, 88, 120
- evolution of, 128–129
 - and flattened leaves, 191
 - and photosynthesis, 86
 - and regeneration, 88–90, 125
- shoot flattening, 166–167, 169, 191
- soil lipid biomarkers, 113–114, 115f
- soil microbial communities, 113–114
- soil quality, 92f, 102
- and acid phosphatase activity, 111
 - and adaptation to drought, 63
 - and competition with angiosperms, 60, 68, 70, 80, 120, 124
 - and growth, 108, 110f, 112f, 112t, 124f, 130t
 - and leaf life span, 123
 - and light, 90–91, 124, 124f
 - and nutrient capture, 122–125, 175–176
 - as poor and podocarp tolerance to, 67, 103–104, 106–109, 129, 190–191
- Solomon Islands, 59t, 61, 72–75t, 132–135
- South America, 21, 71t
- fossil record from, 28, 30, 33, 35, 36, 44
 - and impact of disturbance, 88–89
 - and regeneration, 89, 126–127
 - species distribution in, 44, 45, 47f, 48–50, 54, 68–69, 71, 102, 121, 131
 - species diversity in, 43
- species dispersal, 26, 28, 30, 33–36, 129, 172, 190
- climatic impact on, 31, 33, 36, 37f, 38

- species distribution, 21–22, 58f, 59t, 72–75t, 89, 189–190
 - in Africa, 81–85
 - in Amazonia, 44, 47f, 48
 - in Asia, 33, 57, 60–63, 102, 129–131, 142
 - in Australasia, 131
 - in Australia, 60–62, 151
 - in Central America, 44–46, 48–50, 54
 - in neotropics, 44–45, 190
 - in New Caledonia, 66–67
 - in New Zealand, 46, 58f, 121–122, 125, 127
 - in South America, 44, 45, 47f, 48–50, 54, 68–69, 71, 102, 121, 131
- species divergence
 - chloroplast used to estimate, 9, 11f, 12f
 - time estimation of, 2, 7, 9
- species diversity, 1–3, 72–75t
 - in Africa, 22, 80–81
 - in Asia, 59, 60
 - in Australasia, 129
 - in Australia, 59–60, 72–75t
 - influences on, 59–60
 - in Malesia, 43–44, 57, 58f, 59–60
 - in neotropics, 43–44
- sporophylls
 - production of after fire, 143, 145–146
- stem diameter, *see* “diameter, stem”
- Sulawesi, 35, 59t, 72–75t
- Sumatra
 - endangered species of, 193t
 - and species dispersal, 33, 36, 38
 - species distribution in, 62–63
 - species of, 59t, 61, 72–75t, 132–136, 169
- Sunda Islands, 59t, 72–75t, 132–136
- Taiwan
 - endangered species in, 61, 193t
 - fossil record from, 28
 - species distribution in, 57
 - species of, 59t, 72–75t, 133, 134, 136
- temperature
 - and embolism in cold climates, 86, 171–172
 - and frost resistance, 121–122
 - and hydraulic function in cold climates, 159, 171–172
- temporal stand replacement model, 89–90
- Thailand, 59t, 68, 72–75t, 132–133
- Tonga, 72–75t, 193t
- torus-margo pit, 86
- tracheids, 85–86
- Vanuatu, 59t, 60, 72–75t
- Venezuela
 - endangered species of, 193t
 - species distribution in, 45, 48, 54
 - species of, 49t, 136, 137
- Vietnam
 - fossil record from, 28, 31
 - and species dispersal, 36
 - species of, 59t, 62, 69, 72–75t, 132–133, 135, 136, 170f
- wood density, 120, 123, 169–170

Index of Scientific Names

Page numbers followed by “t” refer to a table; page numbers followed by “f” refer to a figure.

- Acmopyle*, 2
 - distribution of, 59t, 63
 - diversification shift point of, 16f
 - phylogeny of, 8f, 11f
 - shoot flattening of, 17, 166f, 167
- Acmopyle pancheri*, 5t, 65f
 - distribution of, 66–68, 72t
- Acmopyle sabniana*, 72t
 - conservation status of, 193t
 - as endangered, 61
 - phylogenetic analysis of, 5t
- Actinostrobus acuminatus*, 152
- Aesculus*, 178
- Afrocarpus*, 95
 - distribution of, 22, 81–82, 84, 85
 - and divergence time estimation, 9t
 - diversification shift point of, 16f
 - phylogeny of, 7, 8f, 11f, 80
 - shoot flattening of, 17
- Afrocarpus dawei*, 81t
- Afrocarpus falcatus*
 - arbuscular mycorrhizal fungi in, 92, 176
 - dispersal of, 84
 - distribution of, 81t, 85, 86, 91, 95
 - in dry conditions, 122, 129
 - life history properties of, 71t
 - phylogenetic analysis of, 5t
 - phylogeny of, 80
 - regeneration of, 69, 92–94
- Afrocarpus gausсенii*, 5t, 81t
- Afrocarpus gracilior*, 5t, 80, 81
- Afrocarpus mannii*, 5t, 81, 84, 193t
- Afrocarpus usambarensis*, 81t, 193t
- Agathis*, 104, 115, 162
- Agathis australis*, 6t, 178, 181

- Agathis borneensis*, 63, 104
Agathis kinabaluensis, 104, 108, 110f, 111–113
Alisporites, 24, 25f
Alisporites similis, 26
Alnus, 34f
Alseis blackiana, 131
Angophora hispida, 151
Apterocladus, 22
Araucaria, 24, 44, 62, 67, 69, 181
Araucaria angustifolia, 71
Araucaria biramulata, 6t
Araucariacites, 24, 26
Araucaria heterophylla, 6t
Araucaria nemorosa, 68
Archaeospora, 176
Aristotelia serrata, 128
- Beilschmiedia tawa*, 121
Betula, 124
- Callialasporites*, 22
Callitris, 70
Calophyllum, 61
Castanopsis, 62
Casuarina, 31, 32, 124
Cathaysia, 22
Cecropia, 159
Ceiba pentandra, 131
Classopollis, 24–26
Clethra occidentalis, 50, 51
Cryptomeria japonica, 123
Cunonia, 66
Cyrilla racemiflora, 50
- Dacrycarpidites antarcticus*, 23f, 23t
Dacrycarpus
 altitudinal range of, 22, 61, 105, 106, 129
 dispersal of, 33, 36, 38, 190
 distribution of, 59t, 60, 62, 63, 104
 and divergence time estimation, 9t
 diversification shift point of, 16f
 phylogeny of, 7, 8f, 11f
 pollen of, 23
 shoot flattening of, 17, 166f
 and soil lipids, 114t, 115f
Dacrycarpus cinctus, 5t, 61, 72t, 134
Dacrycarpus compactus, 134
 distribution of, 61, 62, 72t
 as fire tolerant, 131
 phylogenetic analysis of, 5t
Dacrycarpus cumingii, 72t, 136
Dacrycarpus dacrydioides, 71t, 126f
 and catastrophic disturbance, 127–128, 131
 phylogenetic analysis of, 5t
Dacrycarpus expansus, 72t, 131, 136
- Dacrycarpus imbricatus*, 70, 101, 105f, 106f, 135
 and acid phosphatase activity, 112
 altitudinal range of, 61, 62, 102, 104–105
 diameter of, 110f
 dispersal of, 33f, 37f
 distribution of, 72t, 131
 life history properties of, 71t
 and nitrogen fixation, 112–113
 phylogenetic analysis of, 5t
 pollen of, 28
 and seed dispersal, 69
 and soil quality, 113, 114, 115f
Dacrycarpus kinabaluensis, 136
 altitudinal range of, 61, 62, 105
 distribution of, 72t, 108
 size of, 110f, 111, 112f
Dacrycarpus linifolius, 9t
Dacrycarpus mucronatus, 9t
Dacrycarpus steupii, 72t, 136
Dacrycarpus vieillardii, 132
 altitudinal range of, 66
 distribution of, 67, 72t
 and disturbance, 131
 phylogenetic analysis of, 5t
Dacrydium
 and acid phosphatase activity, 113–114
 altitudinal range of, 22, 61, 105, 106, 129
 animal dispersal of seeds of, 158
 and arbuscular mycorrhizal fungi, 181
 dispersal of, 36, 37f, 38, 190
 distribution of, 59t, 63
 and divergence time estimation, 9t
 diversification shift point of, 16f
 fire intolerance of, 131
 fossil record of, 30–33
 habitats of, 31–32, 60
 juveniles of, 62
 leaves and stems of, 124
 phylogeny of, 7, 8f, 11f
 pollen of, 23f, 23t, 24, 30
 and soil lipids, 114t, 115f
 and soil quality, 104, 130
Dacrydium araucarioides, 5t, 66, 71t, 72t, 133
Dacrydium balansae, 5t, 66, 67, 72t, 132
Dacrydium beccarii, 31, 61, 73t, 134
Dacrydium comosum, 73t, 135
 conservation status of, 61, 69, 193t
Dacrydium cornwallianum, 61, 63, 73t, 136
Dacrydium cupressinum
 carbon uptake by, 123, 130
 foliage of, 126f
- growth of seedlings of, 127
 life history properties of, 71t
 light use by, 125
 phylogenetic analysis of, 5t
 and regeneration, 128
 roots of, 179f, 183f
Dacrydium elatum, 73t, 133
Dacrydium ericoides, 73t, 135, 193t
Dacrydium franklinii, 24
Dacrydium gibbsiae, 73t, 134
 diameter of, 110f
 and soil quality, 62, 111–112
Dacrydium gracile, 73t, 102, 134
 conservation status of, 193t
 diameter of, 110f, 111f
 and nitrogen fixation, 112–113
 and soil quality, 114, 115f
Dacrydium guillauminii, 65f, 73t, 132
 conservation status of, 193t
 habitats of, 66–67
 phylogenetic analysis of, 5t
 pollen of, 23t, 24
Dacrydium laxifolium, 24
Dacrydium leptophyllum, 61, 73t, 136, 193t
Dacrydium lycopodioides, 5t, 66, 73t, 135
Dacrydium magnum, 73t, 132
Dacrydium medium, 61, 73t, 135
Dacrydium nausoriense, 5t, 61, 73t, 133, 193t
Dacrydium nidulum, 5t, 63, 71t, 73t, 132
Dacrydium novo-guineense, 73t, 131, 135
Dacrydium pectinatum, 61–63, 73t, 104, 130, 132
Dacrydium spathoides, 61, 73t, 135
Dacrydium xanthandrum, 61, 73t, 134
Dasyphyllum diacanthoides, 127
Doryanthes excelsa, 151
- Eidothea hardeniana*, 70
Ephedripites, 26
Eucalyptus, 124, 152
Eucalyptus marginata, 150f
Eucryphia milliganii, 120
Exesipollenites tumulus, 24
- Falcatifolium*, 22, 63, 130
 distribution of, 59t, 60
 and divergence time estimation, 9t
 diversification shift point of, 16f
 phylogeny of, 7, 8f, 11f
 shoot flattening of, 17, 166f, 167
Falcatifolium angustum, 61, 73t, 133, 193t
Falcatifolium falciforme, 73t, 108, 133
 altitudinal range of, 62

- diameter of, 110f, 111f
 life history properties of, 71t
 and nitrogen fixation, 112–113
 phylogenetic analysis of, 5t
 as shade tolerant, 131
 size of, 51, 69–70
Falcatifolium gruezoi, 5t, 73t, 135
Falcatifolium papuanum, 73t, 136
Falcatifolium taxoides, 5t, 66, 73t, 134
 Parasitaxus usta as parasitic to, 67,
 130, 184–185
Ficus, 109, 114
Fitzroya cupressoides, 123
Foliolatus, 8f, 142, 149, 151
- Garcinia*, 61
Ginkgo biloba, 152
Gleichenia bolanica, 62
Glomus, 176
Gnetum, 131, 165
Gymnostoma, 31, 178
Gymnostoma deplancheanum, 66
Gymnostoma nobilis, 31
- Halocarpus*, 9t, 16f, 124
 phylogeny of, 7, 8f, 11f
Halocarpus bidwillii, 5t, 122, 128
Halocarpus biformis, 5t, 123, 125, 126f
Halocarpus kirkii, 5t
Harrisiocarpus, 22
Hedyosmum arborescens, 51
- Isoglossa woodii*, 86, 93
- Juniperus procera*, 176
- Lagarostrobos*, 2, 9t, 16f
 phylogeny of, 7, 8f, 11f
Lagarostrobos franklinii, 120, 123, 171f
 phylogenetic analysis of, 5t
 and regeneration, 127, 128
Laureliopsis philippiana, 127
Lepidothamnus, 16f, 43, 124
 phylogeny of, 7, 8f, 11f
Lepidothamnus fonkii, 5t, 122
Lepidothamnus intermedius, 123, 128,
 179f
Lepidothamnus laxifolius, 5t, 24
Lithocarpus, 62, 103, 114t, 115f
Lithocarpus clementianus, 113, 115f
Lygistepollenites florinii, 23f, 23t, 24
Lyonia octandra, 51
- Macaranga*, 109, 114, 159
Manoao, 9t, 16f, 124
 phylogeny of, 7, 8f, 11f
Manoao colensoi, 5t, 123, 179f
Masculostrobos warrenii, 22
- Mataia podocarpoides*, 9t
Meliclytus ramiflorus, 128
Metapodocarpoxylon, 24
Metasequoia, 167
Metrosideros, 66
Microcachrydites antarcticus, 26
Microcachrys, 2, 23t, 124
 diversification shift point of, 16f
 fossil record of, 35, 36
 phylogeny of, 8f, 11f
Microcachrys antarcticus, 23t, 35
Microcachrys tetragona, 5t
Microstrobos, 2, 124
Microstrobos fitzgeraldii, 5t
Microstrobos niphophilus, 5t
- Nageia*
 dispersal of, 28, 30
 distribution of, 59t
 and divergence time estimation, 9t
 diversification shift point of, 16f
 habitats of, 22, 60, 129
 phylogeny of, 7, 8f, 11f, 80
 pollen of, 23f
 shoot flattening of, 17, 68, 132,
 166–167
Nageia fleuryi, 68–69, 131, 133
 distribution of, 73t
 as endangered, 61
 habitat of, 62
 phylogenetic analysis of, 5t
Nageia formosensis, 5t, 73t
Nageia maxima, 63, 73t, 132, 193t
Nageia motleyi, 62, 132
 distribution of, 73t
Nageia nagi, 133
 distribution of, 73t
 flattened leaves of, 125
 phylogenetic analysis of, 5t
 and regeneration, 128
 sex ratio of, 69
 size of, 51
 and soil quality, 122
Nageia wallichiana, 68, 70, 133
 distribution of, 73t
 habitats of, 61–63, 131
 life history properties of, 71t
 phylogenetic analysis of, 5t
Nemuaron, 66
Nothodacrium, 22
Nothodacrium warrenii, 9t, 22
Nothofagus, 61, 121
Nothofagus grandis, 63
Nothofagus nitida, 126–127
- Oncosperma*, 32
- Palaquium*, 114t, 115f
- Palaquium rioense*, 113, 115f
Pancheria, 66
Pandanus, 63
Papuacedrus, 61
Papuacedrus papuana, 61
Paracryphia, 66
Parasitaxus, 9t, 16f, 59t, 63
 phylogeny of, 7, 8f, 11f
Parasitaxus usta, 5t, 66, 73t, 133
 conservation status of, 68, 193t
 as parasitic to *Falcatifolium taxoides*,
 67, 129–130, 184–185
Pherosphaera, 8f, 11f, 16f
Phyllocladites palaeogenicus, 23f, 23t
Phyllocladus, 3, 102
 dispersal of, 36, 38, 190
 distribution of, 22, 59t, 103
 diversification shift point of, 16f
 phylogeny of, 7, 8f, 11f
 pollen of, 23, 23t, 34–35
 shoot flattening of, 17, 166f, 167
Phyllocladus alpinus, 5t, 122, 128, 177f
Phyllocladus aspleniifolius, 5t
Phyllocladus hypophyllus, 134
 altitudinal range of, 105, 130
 diameter of, 110f
 distribution of, 61, 73t
 leaf nutrients of, 190–191
 phylogenetic analysis of, 5t
 pollen of, 23f
 shoot flattening of, 167
 and soil quality, 111–113
Phyllocladus toatoa, 5t
Phyllocladus trichomanoides, 5t
Picea balfouriana, 123
Pinus, 34f, 124, 158, 169
Pinus cubensis, 46
Pinus krempfii, 169, 170f
Pinus merkusii, 169
Pinus occidentalis, 131
Pinus radiata, 120
Podocarpidites, 23f, 23t, 24, 26
Podocarpoxylon, 26
Podocarpus, 95
 accessory transfusion tissue of, 167
 in Africa, 79–80
 altitudinal range of, 45–46, 48, 61,
 129
 animal dispersal of seeds of, 158
 antimicrobial chemicals in bark of,
 123
 and arbuscular mycorrhizal fungi, 181
 conservation of, 54
 as dioecious, 68
 dispersal of, 28, 29f, 30, 35–36, 38
 distribution of, 25f, 47f, 49t, 57, 59t,
 82, 84
 and divergence time estimation, 9t

Podocarpus (continued)

- diversification shift point of, 16f
- diversity of, 2, 43–44, 60, 63
- as dominant, 87–89, 94
- and fire intolerance, 128
- fossil record of, 22, 26, 30
- habitats of, 22, 60, 129
- phylogeny of, 7, 8f, 11f
- pollen of, 23f, 23t, 24, 28, 158
- shade tolerance of, 132
- shoot flattening of, 17, 166f
- and soil quality, 130
- Podocarpus acuminatus*, 48f, 136
- Podocarpus affinis*, 5t, 61, 73t, 193t
- Podocarpus alpinus*, 5t
- Podocarpus angustifolius*, 45, 46, 54, 193t
- Podocarpus annamiensis*, 5t, 73t
- Podocarpus archboldii*, 73t, 135
- Podocarpus aristulatus*, 5t, 193t
 - distribution of, 45–46, 48f, 49t, 50, 131
- Podocarpus atjehensis*, 73t, 136
- Podocarpus beecherae*, 67, 73t, 133, 193t
- Podocarpus borneensis*, 74t, 136
- Podocarpus bracteatus*, 74t, 136
- Podocarpus brasiliensis*, 44, 136
- Podocarpus brassii*, 6t, 74t, 135
- Podocarpus brevifolius*, 74t, 136, 193t
- Podocarpus buchholzii*, 44, 47f, 48f, 136
- Podocarpus capuronii*, 81, 193t
- Podocarpus celatus*, 45–48f
- Podocarpus chinensis*, 6t, 74t
- Podocarpus chingianus*, 74t
- Podocarpus colliculatus*, 67, 74t
- Podocarpus confertus*, 61, 74t, 132
- Podocarpus coriaceus*, 45, 46, 48f, 54
- Podocarpus costalis*, 6t, 61, 74t, 133, 193t
- Podocarpus costaricensis*, 45, 47f, 48f, 193t
- Podocarpus crassigemmis*, 74t, 135
- Podocarpus cunninghamii*, 6t
- Podocarpus decumbens*, 64f, 66, 67, 74t, 193t
- Podocarpus deflexus*, 74t, 135, 193t
- Podocarpus degeneri*, 74t
- Podocarpus dispermus*, 6t, 62, 74t, 136, 167
- Podocarpus drouynianus*, 69, 141–142
 - distribution of, 143, 144f, 144t
 - as drought resistant, 122, 171
 - as fire resistant, 128
 - growth of, 146
 - leaves of, 142, 149
 - lignotubers of, 146–147, 152–153
 - morphological adaptations of, 151, 153
 - phylogenetic analysis of, 6t
 - population structure of, 149
 - pyrogenic reproduction of, 151, 153
 - and resprouting, 153, 154, 191–192
 - seeds of, 142, 143, 145f, 146, 151–152
 - size of, 150f
 - and soil quality, 152
- Podocarpus elatus*, 6t, 74t
- Podocarpus elongatus*, 6t, 80, 81, 152
- Podocarpus ensiculus*, 80
- Podocarpus fasciculus*, 74t
- Podocarpus gibbsiae*, 61, 74t, 112–113, 135, 193t
- Podocarpus glaucus*, 74t, 135
- Podocarpus globulus*, 61, 74t, 133, 193t
- Podocarpus glomeratus*, 47f, 48f, 136
- Podocarpus gnidioides*, 6t, 66, 74t, 135
- Podocarpus grayae*, 68, 74t, 131, 151, 171f
- Podocarpus guatemalensis*, 6t, 54, 190
 - distribution of, 45, 47–48f, 49t, 50
- Podocarpus hallii*, 71t, 122, 127
- Podocarpus henkelii*, 6t, 80, 81t, 86
- Podocarpus hispaniolensis*, 45, 48f, 49t, 54, 193t
- Podocarpus humbertii*, 47f, 81t, 193t
- Podocarpus ingensis*, 46–48f, 136
- Podocarpus insularis*, 74t, 132
- Podocarpus lambertii*, 6t, 44, 48f, 68–69, 136
- Podocarpus latifolius*, 6t, 68, 80–81, 85f, 95
 - distribution of, 81t, 82f, 86, 94
 - and gap-phase dynamics, 88
 - habitats of, 87, 92
 - life history properties of, 71t
 - regeneration of, 80, 90, 127
 - seeds of, 84, 91f
- Podocarpus laubenfelsii*, 63, 74t, 134, 193t
- Podocarpus lawrencei*, 6t, 71t, 122
- Podocarpus ledermannii*, 74t, 133–134
- Podocarpus levis*, 74t, 134
- Podocarpus longifoliolatus*, 6t, 66, 67, 74t, 193t
- Podocarpus lophatus*, 61, 74t, 136, 193t
- Podocarpus lucienii*, 66, 74t
- Podocarpus macrocarpus*, 74t, 136
- Podocarpus macrophyllus*, 6t, 74t, 136, 180
- Podocarpus madagascariensis*, 81t
- Podocarpus magnifolius*, 45, 47f, 48f, 136
- Podocarpus matudae*, 6t, 69, 137
 - distribution of, 45, 48f, 49t
- Podocarpus micropedunculatus*, 74t, 133
- Podocarpus milanjanus*, 37f, 80–81
- Podocarpus monteverdeensis*, 45
- Podocarpus nakaii*, 61, 74t, 134, 193t
- Podocarpus neriifolius*, 131–133, 136, 170f
 - distribution of, 61, 74t
 - habitats of, 62, 63, 71
 - phylogenetic analysis of, 6t
 - pollen of, 28
 - seeds of, 69
- Podocarpus nivalis*, 6t
- Podocarpus novae-caledoniae*, 65f, 66, 67, 74t
- Podocarpus nubigenus*, 6t, 71t, 123, 126–127
- Podocarpus occidentalis*, 45
- Podocarpus oleifolius*, 45–49, 54
- Podocarpus palawanensis*, 74t, 193t
- Podocarpus pallidus*, 61, 74t, 193t
- Podocarpus parlatorei*, 45, 47f, 48f
- Podocarpus pendulifolius*, 48f, 193t
- Podocarpus perrieri*, 81, 193t
- Podocarpus pilgeri*, 61, 74t
- Podocarpus polyspermus*, 66, 74t, 131, 193t
- Podocarpus polystachyus*, 6t, 28, 74t, 133
- Podocarpus pseudobracteatus*, 74t, 134
- Podocarpus purdieanus*, 45, 50, 54, 193t
- Podocarpus ridleyi*, 74t, 135
- Podocarpus roraimae*, 47f, 48f, 137
- Podocarpus rostratus*, 81, 193t
- Podocarpus rotundus*, 75t, 134
- Podocarpus rubens*, 75t, 134
- Podocarpus rumphii*, 6t, 75t, 136
- Podocarpus rusbyi*, 47f, 48f
- Podocarpus salignus*, 6t, 123
- Podocarpus salomoniensis*, 75t
- Podocarpus sellowii*, 44, 47f, 48f, 49t, 136
- Podocarpus smithii*, 6t, 75t, 134
- Podocarpus spathoides*, 61, 75t, 134
- Podocarpus spinulosus*, 129, 134, 141–142
 - chichi structure of, 152, 153
 - distribution of, 143, 144f, 144t
 - as fire resistant, 128
 - growth of, 146
 - leaves of, 142, 149
 - lignotubers of, 146–147, 153
 - morphological adaptations of, 151, 153
 - phylogenetic analysis of, 6t
 - population structure of, 149, 151
 - reproduction of, 151
 - and resprouting, 152–154

- seeds of, 142, 143, 145f
and soil quality, 152
stems of, 142, 147–149
Podocarpus sprucei, 44, 47f, 48f, 49t, 137
Podocarpus steyermarkii, 47f, 48f, 137
Podocarpus strzeleckianus, 9t
Podocarpus subtropicalis, 75t
Podocarpus sylvestris, 6t, 66, 67, 75t
Podocarpus tepuiensis, 44, 45, 47f, 49–50, 137
Podocarpus teysmannii, 75t, 133
Podocarpus totara, 6t, 71t, 120–122, 182f
and catastrophic regeneration, 127–128, 131
Podocarpus trinitensis, 45, 54
Podocarpus urbanii, 134–135
distribution of, 45, 48f, 49t, 50
growth of, 130
leaf nutrients of, 190
mortality rates of, 52–54
and soil quality, 50–52
Podocarpus woltzii, 81, 137
Protophyllocladoxylon, 24
Prumnopitys, 4, 181
dispersal of, 28, 30
distribution of, 22, 43, 45, 59t, 63
and divergence time estimation, 9t
diversification shift point of, 16f
habitats of, 60
phylogeny of, 7, 8f, 11f
pollen of, 23f
shoot flattening of, 17, 166f
Prumnopitys andina, 6t
Prumnopitys exigua, 45
Prumnopitys ferruginea, 6t, 126f
life history properties of, 71t
regeneration of, 125, 127
root system of, 177f, 184
Prumnopitys ferruginoides, 6t, 66, 67, 75t
Prumnopitys harmsiana, 45, 54
Prumnopitys ladei, 6t, 71t, 75t, 136
Prumnopitys limaniae, 9t
Prumnopitys montana, 45, 137
Prumnopitys opibiensis, 9t
Prumnopitys standleyi, 45, 136
Prumnopitys taxifolia, 6t, 71t, 126f, 127–128
Quercus, 44
Quintinia, 66
Rapanea vaccinioides, 62
Retrophyllum, 80
distribution of, 28, 43, 45, 59t, 63, 66
and divergence time estimation, 9t
diversification shift point of, 16f
phylogeny of, 7, 8f, 11f
shoot flattening of, 17, 166f
Retrophyllum comptonii, 6t, 63, 135
distribution of, 66, 67, 75t
Retrophyllum minus, 64f, 66–67, 75t, 133, 193t
Retrophyllum rospigliosii, 45, 54, 136, 193t
Retrophyllum vitiense, 6t, 75t
Rhizobium, 180
Rhizophora, 32
Rhus tomentosa, 87
Rissikia, 9t, 22
Rugubivesiculites reductus, 26
Saxegothaea, 17
distribution of, 2, 43
diversification shift point of, 16f
phylogeny of, 8f, 11f
pollen of, 22, 24, 36
Saxegothaea conspicua, 6t, 71t, 123, 126–128
Scarburgia, 22
Sciadopitys, 178
Sequoia, 167
Shorea ovata, 63
Shorea revoluta, 63
Sphenostemon, 66
Stalagma samara, 22
Stirlingia latifolia, 151
Sundacarpus
distribution of, 59t, 60
phylogeny of, 4, 7, 8f, 11f
shoot flattening of, 166f, 167
Sundacarpus amarus, 6t, 69, 135
distribution of, 61–63, 75t
Synoum, 151
Syzygium, 103
Tasmannia lanceolata, 159
Taxodium, 167
Taxus, 158
Telopea speciosissima, 151
Toona australis, 131
Trimenia, 66
Trisaccites, 23
Tristaniopsis, 103, 113, 114t, 115f
Tsuga, 24
Tsuga sieboldii, 123
Vaccinium meridionale, 50
Weinmannia, 44
Weinmannia racemosa, 128
Weinmannia trichosperma, 126–127
Widdringtonia nodiflora, 152
Wollemia, 176
Zygogynum, 66

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